CHARACTERIZATION OF POST-MORTEM SHELL ALTERATION IN ARANSAS BAY, TEXAS

A Thesis

by

DAVID EDWARD SCHIRM

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

Chair of Committee,	Thomas Olszewski
Committee Members,	Michael Tice
	Daniel Thornton
Head of Department,	John R. Giardino

August 2013

Major Subject: Geology

ABSTRACT

Accumulations of dead shells in both modern coastal settings and in the rock record contain valuable information on past ecosystems and environmental conditions. However, death assemblages are not simply snapshots of living communities; rather, the abundances of different species have been biased due to differential rates of postmortem destruction. In order to constrain the nature and degree of bias in modern molluscan death assemblages in a shallow marine environment, I deployed mesh-bag experiments including six species of bivalves into a natural marine environment on the Texas coast. The mesh bag design for tethering shells allowed for maximum exchange between ambient environmental conditions and the shells while the apparatus was deployed. The apparatuses were recovered after 2 weeks, 4 weeks, 8 weeks, 16 weeks, 8 months, and 12 months. Shells were examined under a Scanning Electron Microscope (SEM) to analyze integrity, document degradation, and investigate patterns of biological, chemical, and physical abrasion and destruction. SEM analysis indicates that some shells clearly degraded, while others did not, even after 12 months. In addition, epifaunal shells experienced postmortem encrustation by sessile organisms more than infaunal shells, indicating a species-level preservational bias.

ACKNOWLEDGEMENTS

I would like to thank my committee chair, Dr. Olszewski, and my committee members, Dr. Thornton, and Dr. Tice, for their guidance and support throughout the course of this research.

Thanks also to my friends and colleagues and the department faculty and staff for making my time at Texas A&M University a great experience. I also want to extend my gratitude to the National Science Foundation, which provided the funding, Dr. Michael Pendleton, Dr. Ray Guillemette, Mark Fischer and the Texas Parks and Wildlife Department in Rockport, TX, and Adam Lee.

Finally, thanks to my mother and father for their unwavering support and encouragement.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

Page

1. INTRODUCTION

Fossil assemblages are a central tool paleontologists have for understanding ecological systems in the past. A fundamental aspect of any ecological system is the number and abundances of its member species. Because different species have different levels of preservability, species' richness and relative abundances can be altered as their dead remains pass into the rock record. Such preservational bias has been called upon to explain large-scale changes in the fossil record (e.g., Kidwell and Brenchley, 1994) as well as discrepancies between living communities and modern death assemblages (Cummins et al., 1986; Staff et al., 1986). However, direct measurement of shell ages suggests that differential rates of loss are not a significant factor in biasing species' abundances in shelly marine accumulations (Krause Jr. et al., 2010; Kosnik et al., 2009). In order to infer past ecological processes from modern death and ancient fossil assemblages, paleoecologists must develop a process-based understanding of the origin of species-specific preservational bias.

Time-averaging is the mixing of shells that lived at different times and possibly different locations but have been deposited together. It is a ubiquitous feature of death assemblages. Over geologic time, reproduction, metabolic output, and hard-part durability have increased in benthic communities (Kidwell and Brenchley, 1994), which suggests that over time there has been an increase in time-averaging in death assemblages. Several previous studies of shelly marine invertebrates (Miller, 1988; Warme et al., 1969; Peterson, 1976) found that death assemblages reflect the living assemblage from which they were derived. Kidwell (2001) found that time-averaged death assemblages parallel species' original rank orders in life. In addition, she found that species that are abundant in the death assemblage are abundant in the living assemblage and those species that are rare in the death assemblage are rare alive (Kidwell, 2002). In contrast, Cummins et al. (1986) found that animal hard-parts do not accumulate in the death assemblage at the same rate at which animals die. Since not every shell makes it into the death assemblage, there must be a reason or reasons why some find their way into it and others do not. The sources and mechanisms of this bias are debated, but models suggest that post-mortem shell age distributions depend on how long a shell stays in the first few centimeters of the sediment column, in which a shell can be modified or destroyed in the taphonomically active zone (TAZ) (Olszewski, 2004). We know from previous tethering experiments that environments of deposition have an effect on hard-part weathering, but not in a predictable manner (Callender et al., 2002). Flessa and Kowalewski (1994) showed that offshore environments typically have older shells than nearshore environments, implying that the more dynamic nearshore systems have higher rates of destruction or more rapid burial. This was further validated when Carroll et al. (2003) used amino acid racemization to date mollusk shells and concluded that intrinsic species characteristics are not the principle factors controlling time-averaging, and that extrinsic environmental factors and intrinsic local fluctuations in population density are more likely the governing factors that control time-averaging and dead abundance.

Recently, there has been some disagreement about the mechanisms of the bias found in death assemblages. Kosnik et al. (2009) showed that shell durability characteristics such as size, thickness, and density play a large role in determining a shell's likelihood to be preserved. In contrast, Behrensmeyer et al. (2005) found no such correlation in a survey of the literature, suggesting that small, thin shells were just as likely to be preserved as heavy, robust ones. In addition, site specific differences were more likely to have an impact on death assemblages than intrinsic shell characteristics according to Krause Jr. et al. (2010).

While depositional and post-depositional factors may have some effect on the bias found in death assemblages, it is likely that innate physical and chemical properties of different species are an important factor in determining their abundances in death assemblages, because shells with different mineralogical composition and microstructure are expected to degrade at different rates. The aim of this study was to test this hypothesis experimentally in the field by using six different bivalve species with different shell microstructures placed under the same physical conditions. Specimens were retrieved periodically over 12 months, weighed to assess shell loss, and examined using a scanning electron microscope (SEM) to characterize the nature of any changes. The purpose of using an SEM was to find patterns in the breakdown of shells related to microstructure and composition. If the hypothesis that differences in mineralogy and microstructure affect rates of postmortem loss is correct, each species will show differences in the amount and type of degradation that has taken place. If the hypothesis is incorrect, species will show only small or inconsistent differences in the amount of degradation, which would indicate that the rate of post-depositional alteration is due to environmental factors independent of species identity, such as sedimentation rate, sediment reworking, and pore water chemistry.

2. METHODS

This experiment focused on changes in the mass and alteration of six species of bivalves: *Amygdulum papyrum, Mulinia lateralis, Ischadium recurvum, Macoma mitchelli, Crassostrea virginica, and Rangia cuneata* (Fig. 1). The six species differ in shell microstructures and mineralogies (Taylor et al. 1999, 1973): *I. recurvum* and *A. papyrum* (superfamily Mytilacea) have two layers of nacreous aragonite, *C. virginica* (superfamily Ostreacea) is composed of foliated calcite, and *Mu. lateralis*, *R. cuneata*, (superfamily Mactracea) and *Ma. mitchelli* (superfamily Tellinacea) consist of two layers of cross-lamellar aragonite.

Live bivalves were collected to ensure taphonomically unmodified shells were used in the experiment. After collection, soft tissues were removed and the shells were rinsed in fresh water. Shells were then numbered and sorted and arranged according to species. *Rangia* and *Crassostrea*, which have large and robust shells, were cut into pieces using a rock saw because whole shells were too big to be analyzed under the SEM. The dry weight of both valves of every specimen was recorded. One valve was deployed (the other was kept for reference) in fiberglass mesh bags allowing water and sediment exchange with the surrounding environment; larger shells (*Rangia, Crassostrea,* and *Ischadium*) were placed in bags with a 2 x 2 mm mesh and smaller shells (*Amygdulum*, *Macoma*, and *Mulinia*) placed in bags with a 1 x 2 mm mesh (Figure 2). Each shell was given its own pouch to ensure that no shell-on-shell damage occurred

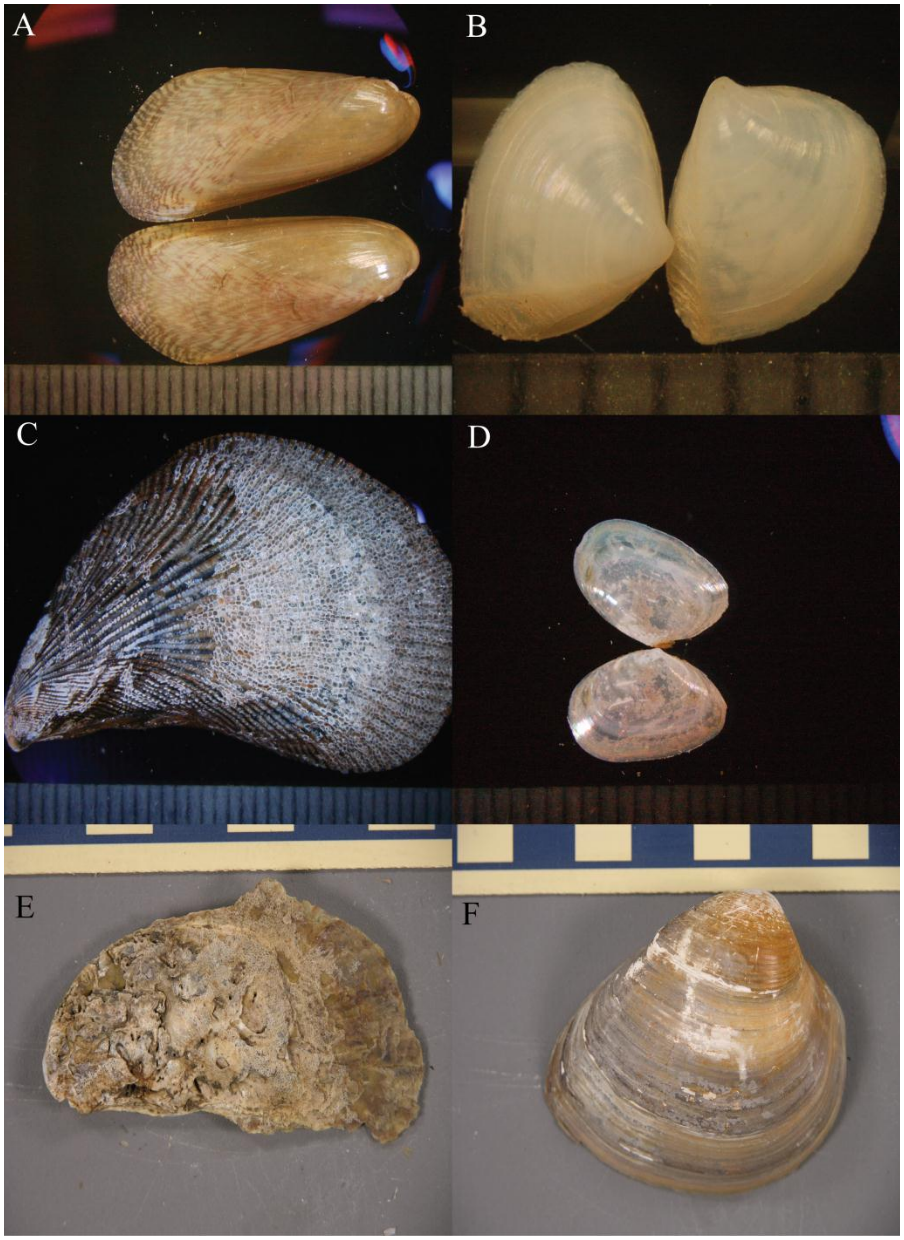

Figure 1, Images of shells used in experiment. A, *Amygdulum*; B, *Mulinia*; C, *Ischadium*; D, *Macoma*; E, *Crassostrea*; F, *Rangia* (Scale in A-D in mm; Scale in E-F in cm)

during the experiment. The shell confinement apparatus consisted of PVC pipe assembled in the shape of a staple. The crossbar is approximately 1.21 meters long and the legs on both sides are 0.61 meters in length. Two holes were drilled 1.9 cm apart on the cross bar to tether the shell bags. Four sets of 2 holes (8 holes total) were drilled on each crossbar equidistant from one another and on alternating sides of the crossbar. Each tether holds 4 to 5 shell bags. Bags were kept track of using a legend; distinguishing marks on the apparatus indicated which bag was which.

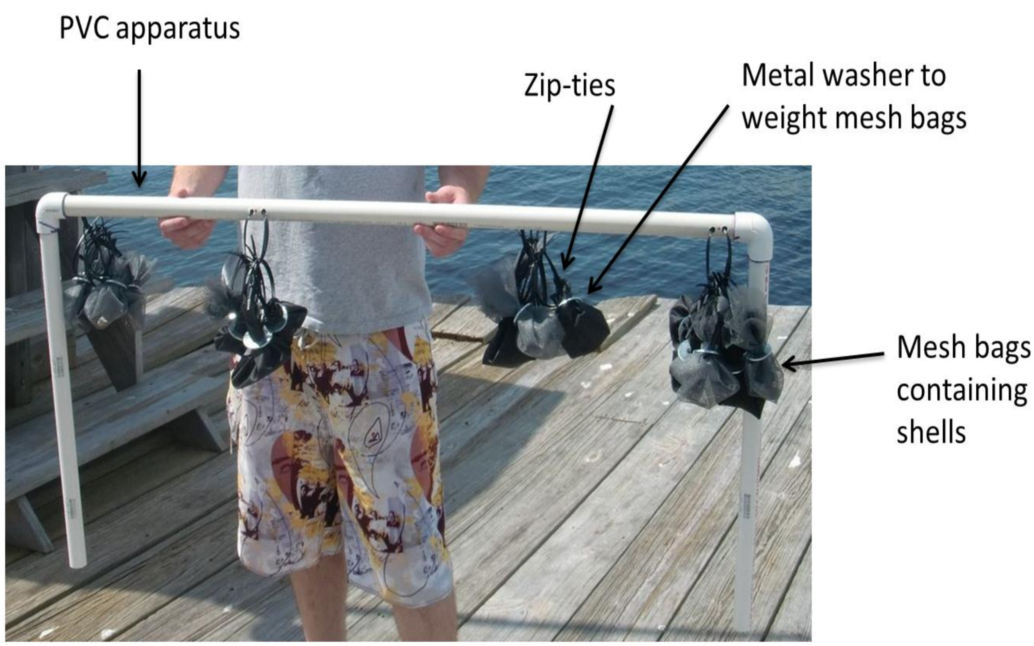

Figure 2, PVC pipe apparatus. Each shell is in its own mesh bag with a metal washer on top to weight the bag and keep it on or below the sediment surface.

Seven apparatuses were deployed in Aransas Bay next to the Texas Parks and Wildlife building in approximately 5 feet of water on September 17th a t . , . (Figure 3). A single apparatus with all its tethered specimens was retrieved at 2, 4, and 8 weeks, 4 months, 8 months, and 1 year. Shells retrieved from the field were washed and weighed. Afterwards, the shells were gold coated for imaging on the scanning electron microscope (SEM). Acquisition of images with a JEOL JSM-6400 SEM allowed for examination of the surface of each shell with a focus on chemical and physical degradation. All images were taken between x10 and x1000 magnification using a standard of fifteen kilovolts of accelerating voltage.

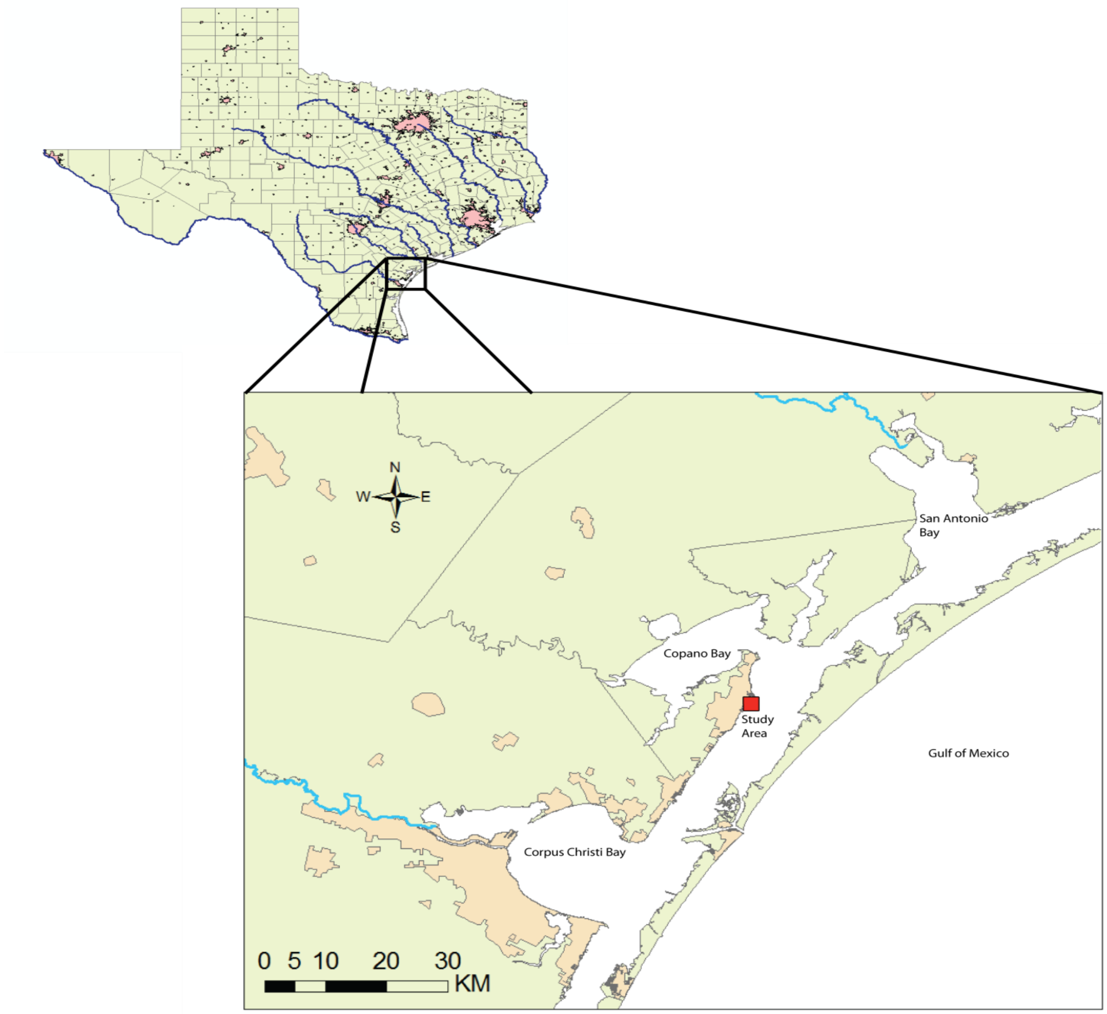

Figure 3, Map of study area

3. RESULTS

Post-mortem Alteration

In order to help identify types of alteration on field specimens, several lab experiments were performed on taphonomically unaltered shells. The first was a scratch test, in which a *Crassostrea,* an *Ischadium*, and a *Rangia* shell were each rubbed with 100 grit sandpaper (average particle size of 162 μm for 1 minute in order to identify the characteristics of physical abrasion. In the next experiment, a *Crassostrea*, and *Ischadium*, and a *Rangia* shell were each put into 100 mL of 10 % HCl solution for one hour in order to identify the characteristics of chemical dissolution. The same experiments were attempted on *Amygdulum*, *Macoma*, and *Mulinia* shells, but these species either disintegrated in solution or were too fragile to survive the scratch test. These conditions were chosen to simulate the conditions in Cummins et al. (1986), in which, shells along the Texas coast were described as having a post-mortem half-life of less than one year. The shells in the Cummins et al. (1986) experiment were sampled over a two and a half year period. These shells were exposed for 30 months. Because it would be impractical to leave a shell in a low molarity acid solution for months at a time, a relatively high molarity and short-time span was chosen. The characteristics of chemical dissolution, as seen from the acid test, are small flaking of large areas and pockmarks in close proximity (Figure 4A). The characteristics of physical abrasion, as seen from the scratch test, are exposure of the inner crystalline structure in irregular patches and the generation of groove marks in the shell (Figure 4B).

Physical alterations found in field deployed shells included peeling back of the periostracum (Figure 4C), cracking and chipping of outer layers (Figure 4D), and cementation of sediment grains (Figure 4E). Biological alteration consisted primarily of encrustation by bryozoans (Figure 5A), barnacles (Figure 5B), serpulid worms (Figure 5C), mussels (byssal threads; Figure 5D), and oysters (Figure 5E).

General Patterns of Postmortem Alteration

Postmortem shell alteration increased in frequency and extent with time in all studied species. The number of shells with cemented sediment grains gradually increased over time as did the amount of abrasion to the outside of the shell (Table 1).

Amygdulum and *Ischadium*, the two species with nacreous aragonite shells, both experienced more cracking and peeling of outer layers compared to species with different microstructures. *Crassostrea*, the only species in the experiment with a foliated calcite microstructure, showed no signs of abrasion throughout its entire deployment. Encrustation was almost a ubiquitous feature of larger shells (*Crassostrea*, *Ischadium*, and *Rangia*) and nowhere to be found on smaller shells. Smaller shells (*Amygdulum*, *Macoma*, and *Mulinia*) were also fractured and broken, larger shells were not.

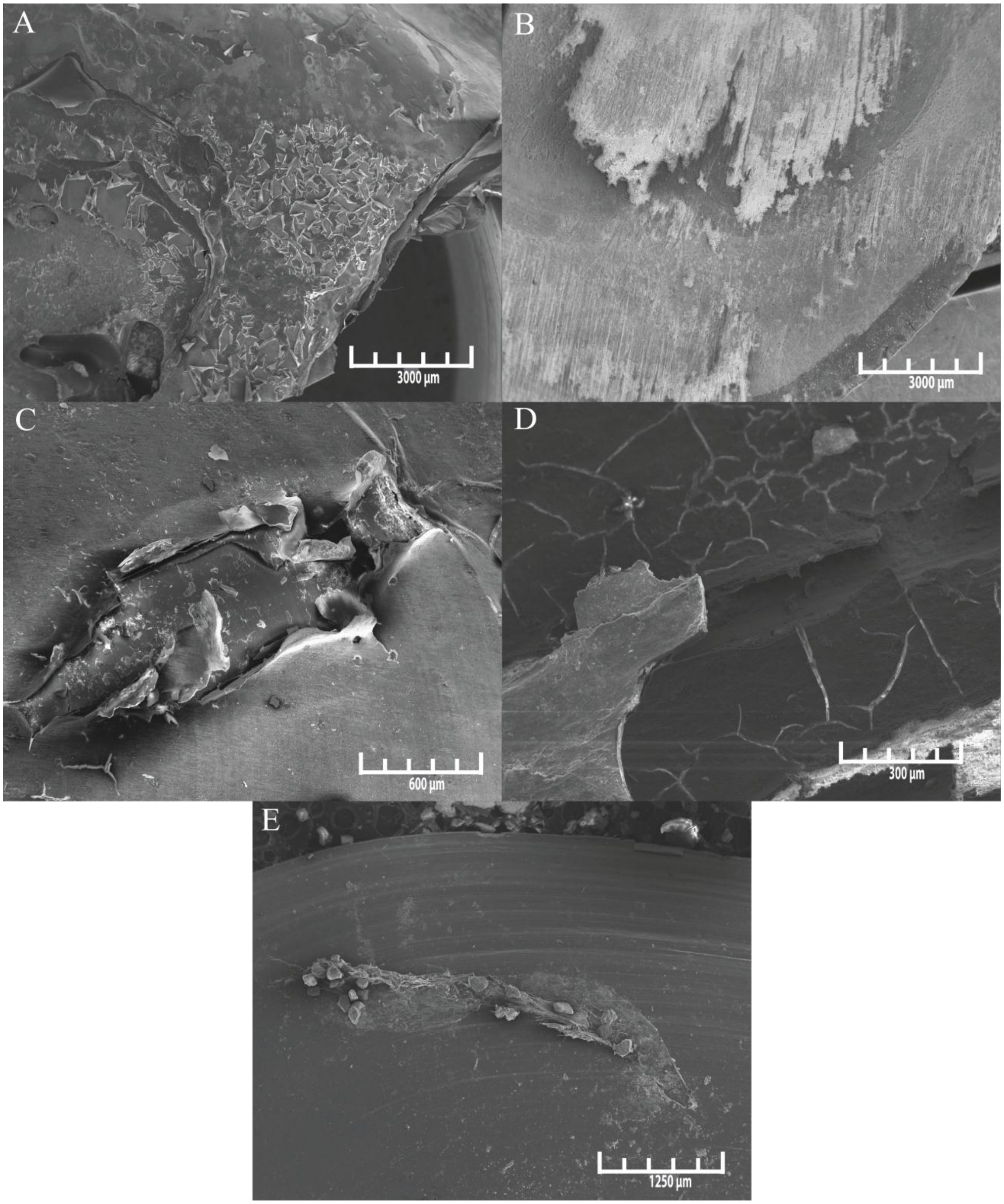

Figure 4, Images of damage to shells. A, Small flaking of large areas from acid test on a *Crassostrea* shell; B, Abrasion marks on an *Ischadium* shell from sand paper test; C, Peeling back of periostracum on an *Amygdulum* shell; D, Cracking and chipping of outer layers of a *Rangia* shell; E, Cemented sediment grains on a *Macoma* shell

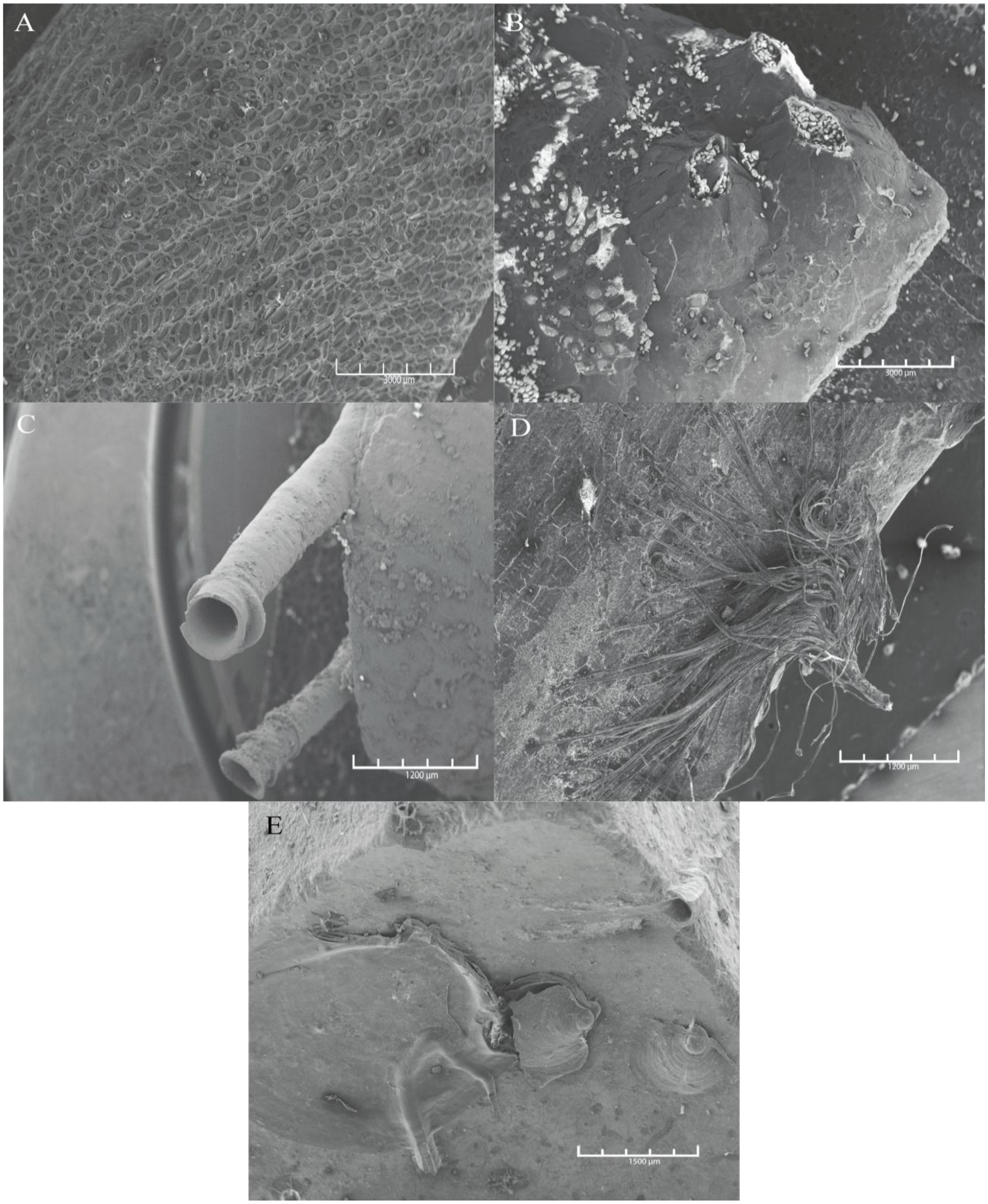

Figure 5, Images of encrusters to shells. A, Bryozoan matrix on the exterior of an *Ischadium* shell; B, Three barnacles on the exterior of a *Crassostrea* shell; C, Two serpulid worms; D; Byssal threads from a mussel; E, Three oysters cemented to a *Rangia* shell

	2 Weeks	4 Weeks	8 Weeks	4 Months	8 Months	1 Year
Amygdulum	• Abrasion patterns • Pieces of shell missing • Peeling of outer layers • Flaking edges • Cemented sediment grains on interior	• Abrasion patterns • Flaking edges • Peeling outer layers • Cemented sediment grains on interior	• Broken shells • Abrasion patterns • Peeling outer layers • 1 shell was broken and rolled up in outer layers • 1 shell had sediment grains cemented on the interior	• Broken shells • Abrasion patterns • Rough texture • Cracking and flaking outer layers • 1 shell had sediment grains cemented on the exterior	• Broken shells • Abrasion patterns • Peeling outer layers • Flaking edges • Cemented sediment grains on exterior	• Broken shells • Abrasion patterns • Flaking edges • Cemented sediment grains on exterior
Crassostrea	• Bryozoan matrix • Cracks in outer layers • Smooth internal texture • Cemented sediment grains on exterior	• Smooth internal texture • Byssal threads • Rough external texture • 1 shell had a bryozoan matrix, barnacles, and serpulid worms • Cemented sediment grains on exterior	• Barnacles • Bryozoan matrix • Serpulid worms • Cemented sediment grains on interior	• Bivalves • Bryozoan matrix • Cemented sediment grains on exterior	• Bryozoan matrix • Smooth internal texture • Cemented sediment grains on exterior and interior	• Bryozoan matrix • Bivalves • Boring holes • Cemented sediment grains on exterior • 1 shell had bivalve encrustations • 1 shell had a serpulid worm network
Ischadium	• Bryozoan matrix • Abrasion patterns • Cracking and flaking of length-wise ridges • All shells had sediments cemented to the exterior • 1 shell had sediment grains cemented to the interior	•Bryozoan matrix •Abrasion patterns •Cracking and flaking of length-wise ridges • 3 shells had sediment grains cemented to interior • All shells had sediment grains cemented to exterior	• Bryozoan matrix • Abrasion patterns • Flaking edges • Cracking and flaking of length-wise ridges • 1 shell had sediment grains cemented to the interior	• Bryozoan matrix • Abrasion patterns • Flaking edges • Peeling of length-wise ridges • 1 shell had sediment grains cemented to interior and exterior • 1 shell had sediment grains cemented to exterior	• Bryozoan matrix • Abrasion patterns • Flaking edges •Cracking and flaking of length-wise ridges • 1 shell had sediment grains cemented to interior	• Bryozoan matrix • Abrasion patterns • Flaking edges • Cracking of lengthwise ridges • 3 of 4 shells had sediment grains cemented to interior • 3 of 4 shells had sediment grains cemented to exterior
Macoma	• Abrasion patterns • 2 of 4 shells had sediment grains cemented to interior • 2 of 4 shells had sediment grains cemented to exterior	• Abrasion patterns • Flaking edges • 1 of 2 shells had sediment grains cemented to interior	• Abrasion patterns • Flaking edges • 2 of 2 shells had sediment grains cemented to interior	• Abrasion patterns • Flaking edges • 3 of 4 shells had sediment grains cemented to interior • 3 of 4 shells had sediment grains cemented to exterior	•Abrasion patterns •Flaking edges • 1 shell was broken • 3 of 3 shells had sediment grains cemented to interior • 1 of 3 shells had sediment grains cemented to exterior	• Broken shells • Abrasion patterns • Flaking edges • 2 of 2 shells had sediment grains cemented to interior • 1 of 2 shells had sediment grains cemented to exterior
Mulinia	• Abrasion patterns	• Abrasion patterns • 1 of 3 shells had sediment grains cemented to interior	• Abrasion patterns	• Abrasion patterns • Flaking edges • 3 of 4 shells had sediment grains cemented to interior • 1 of 4 shells had sediment grains cemented to exterior	•Abrasion patterns • 2 of 3 shells had sediment grains cemented to interior • 1 of 3 shells had sediment grains cemented to exterior	• Abrasion patterns • Missing outer layers • 3 of 4 shells had sediment grains cemented to interior • 3 of 4 shells had sediment grains cemented to exterior
Rangia	• Abrasion patterns • Cracking and flaking outer layers • 1 of 2 shells had sediment grains cemented to interior • 1 of 2 shells had sediment grains cemented to exterior	• Abrasion patterns • Cracking and flaking outer layers • Bryozoan matrix • 1 of 2 shells had sediment grains cemented to interior	• Abrasion patterns • 1 of 2 shells had sediment grains cemented to interior • 2 of 2 shells had sediment grains cemented to exterior	• Abrasion patterns • Serpulid worms • Byssal threads • Bivalves • Cracking & flaking outer layers • 2 of 2 shells had sed. grains cemented to int. • 2 of 2 shells had sed. grains cemented to exterior	• Abrasion patterns • Serpulid worms • Byssal threads • Bivalves • Barnacles • 2 of 2 shells had sediment grains cemented to interior • 2 of 2 shells had sediment grains cemented to exterior	• Abrasion patterns • Serpulid worms • Bryozoan chain • 1 of 2 shells had sediment grains cemented to interior • 2 of 2 shells had sediment grains cemented to exterior

Table 1, Alterations to each species by time deployed in the field.

Amygdulum

Amygdulum is a very thin, nacreous shell. Specimens displayed abrasion patterns, flaking of outer layers around the edges of the shell, and sediment grains cemented to the interior (Table 1). In addition, the exterior of the shell was also peeled back exposing the inner crystalline structure (ICS). All of these features increased in intensity and areal extent throughout deployment. After four weeks, broken shells were also a ubiquitous feature of *Amygdulum*.

Crassostrea

Crassostrea is a large shell composed of foliated calcite. Rather than degrading, like *Amygdulum* shells, *Crassostrea* specimens experienced additions to their shells in the form of biological encrusters (Table 1). These encrusters were the bulk of the observed alterations. Other alterations included cracks around the edges and sediment grains cemented to the shell.

Ischadium

Alterations to the *Ischadium* shells were more subtle than other shells in the experiment. Virtually every *Ischadium* shell started the experiment with some sort of bryozoan growth on the exterior of its shell (Table 1), which appear to have protected the shell from postmortem degradation. Even after a year, the bryozoan growths still covered the shells (Table 1). As time went on, the interior of the shells underwent alteration in the form of abrasion and cemented sediment grains.

Macoma

Like Amygdulum, Macoma is a very thin shell, but it consists of cross-lamellar aragonite rather than nacreous aragonite. Abrasion patterns and sediment grains cemented to both the interior and exterior appeared by two weeks of exposure and persisted for the rest of the deployment (Table 1). Breakage of a single shell did not occur until 8 months of deployment.

Mulinia

Mulinia, a small shell composed of cross-lamellar aragonite, had only abrasion patterns for the first 8 weeks, with the exception of one shell, which had sediment grains cemented to the interior (Table 1). From the four month shells and on, the instances of cemented sediment grains and flaking edges increased.

Rangia

Rangia is a large shell with cross-lamellar microstructure. Up to and including eight weeks, *Rangia* shells displayed abrasion patterns, cracking and flaking of outer layers, and sediment grains cemented to both the interior and exterior of the shells (Table 1). After four months, biological encrusters began to colonize the shells.

Collected Copano Bay *Mulinia*

In order to compare and contrast the alteration seen in the experiment with natural alteration, eleven *Mulinia* from sediment grabs taken from a variety of locations in Copano Bay were chosen to be analyzed under the SEM.

The amount of alteration to the surface area of the collected shells is comparable to the shells in the experiment (Figure 6). One shell had almost no visible alteration, while several other shells had alterations on almost every part of the shell. The collected

Mulinia had similar alterations to the *Mulinia* shells in the experiment; abrasion, a few cemented sediment grains, chipped edges, and missing outer layers. The collected *Mulinia* also had small pockmarks, a type of alteration that was not seen on the shells in the experiment (Figure 7). This could be evidence of chemical dissolution.

Shell Mass

Figure 8 shows plots of shell mass before deployment and after retrieval. Initially, shells showed little change, and it is not until 16 weeks into the experiment that the first signs of significant shell loss occur: the smaller shells begin to lose mass and a few of the larger shells gain mass due to encrustation. Significant losses of mass represent breakage resulting in only a fragment of the original species being recovered. Gains in mass are associated with postmortem encrustation.

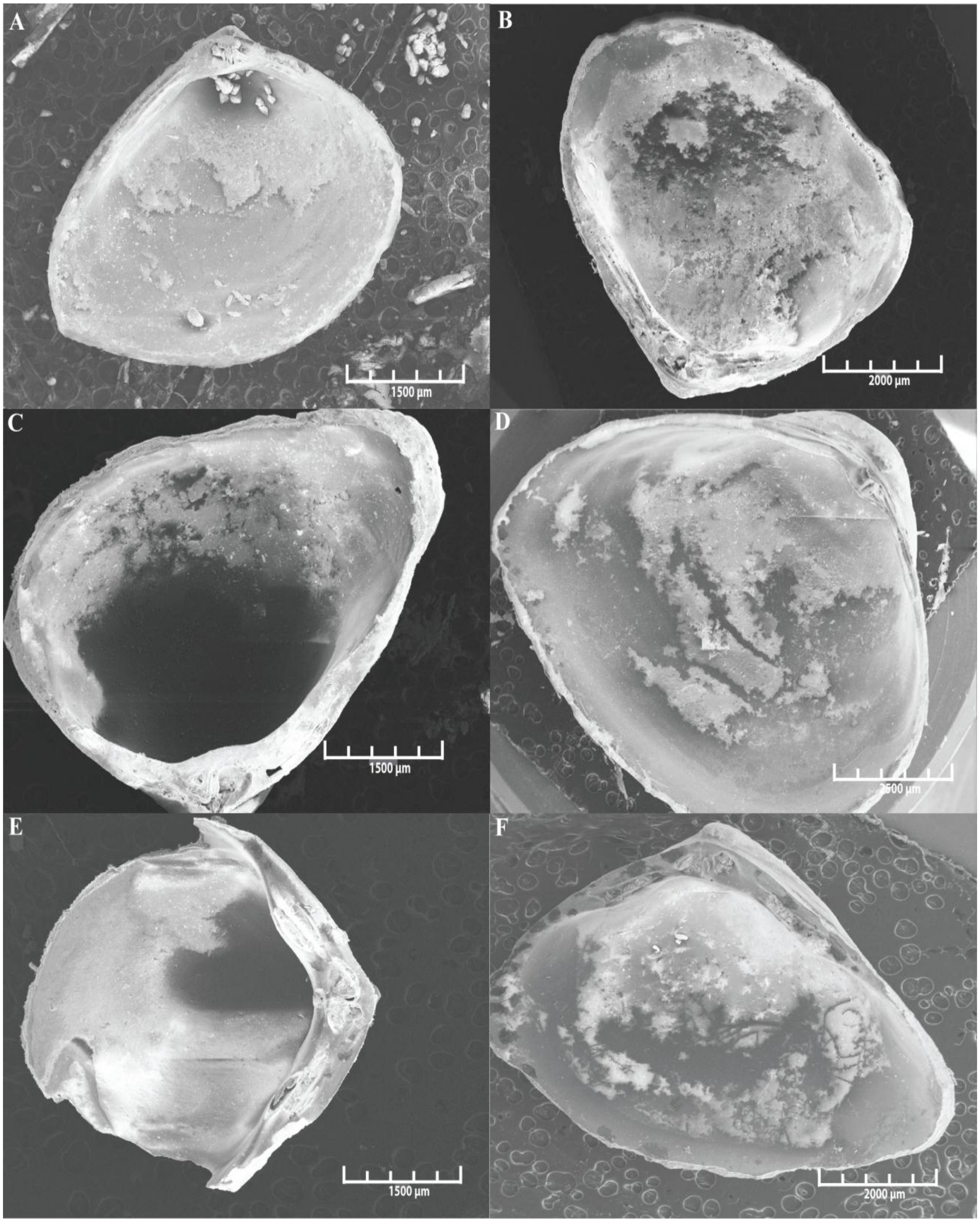

Figure 6, Interior of Mulinia shells. A, The interior of a 4 month Mulinia from the experiment; B, C, D, E, & F, the interiors of Mulinia collected from Copano Bay

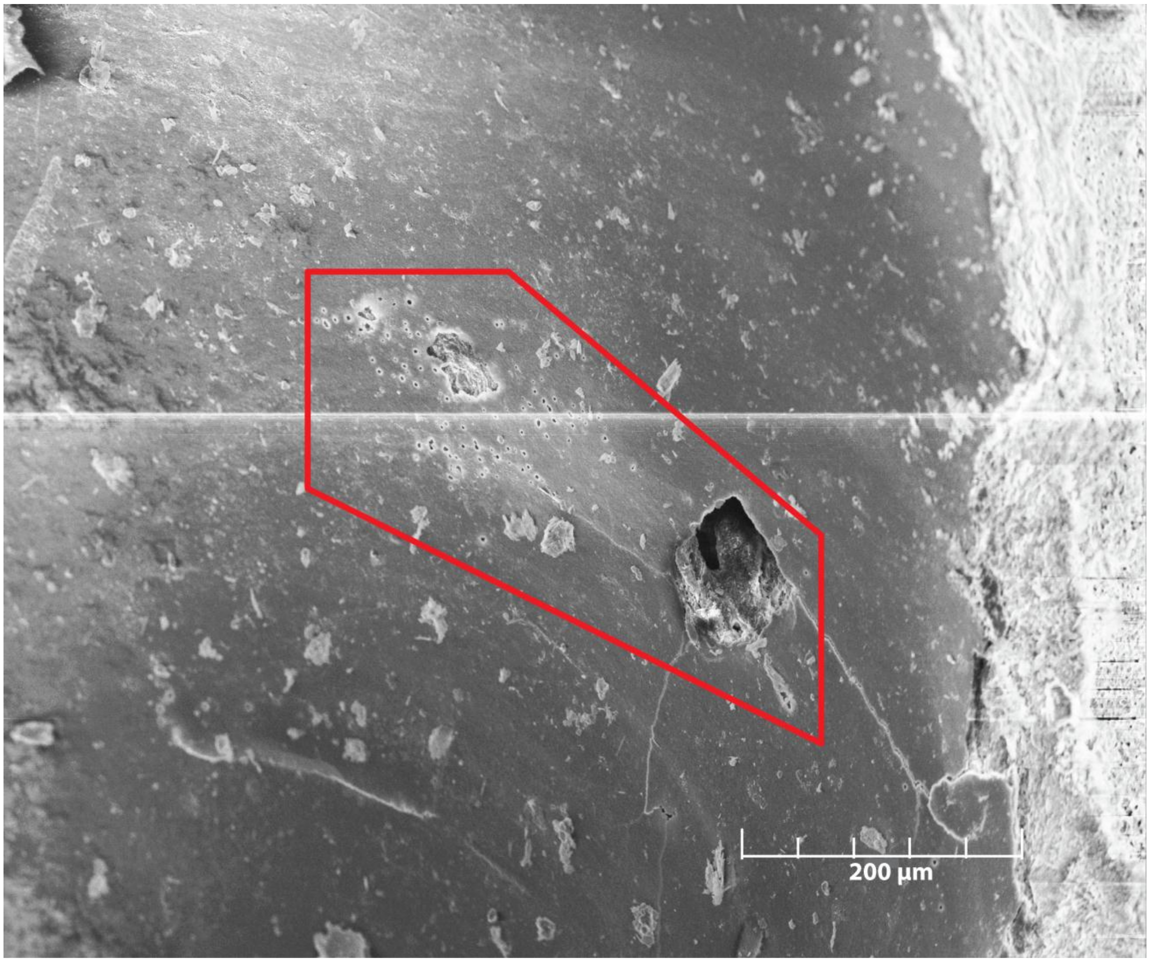

Figure 7, Pockmarks on the interior of a Mulinia shell collected in Copano Bay

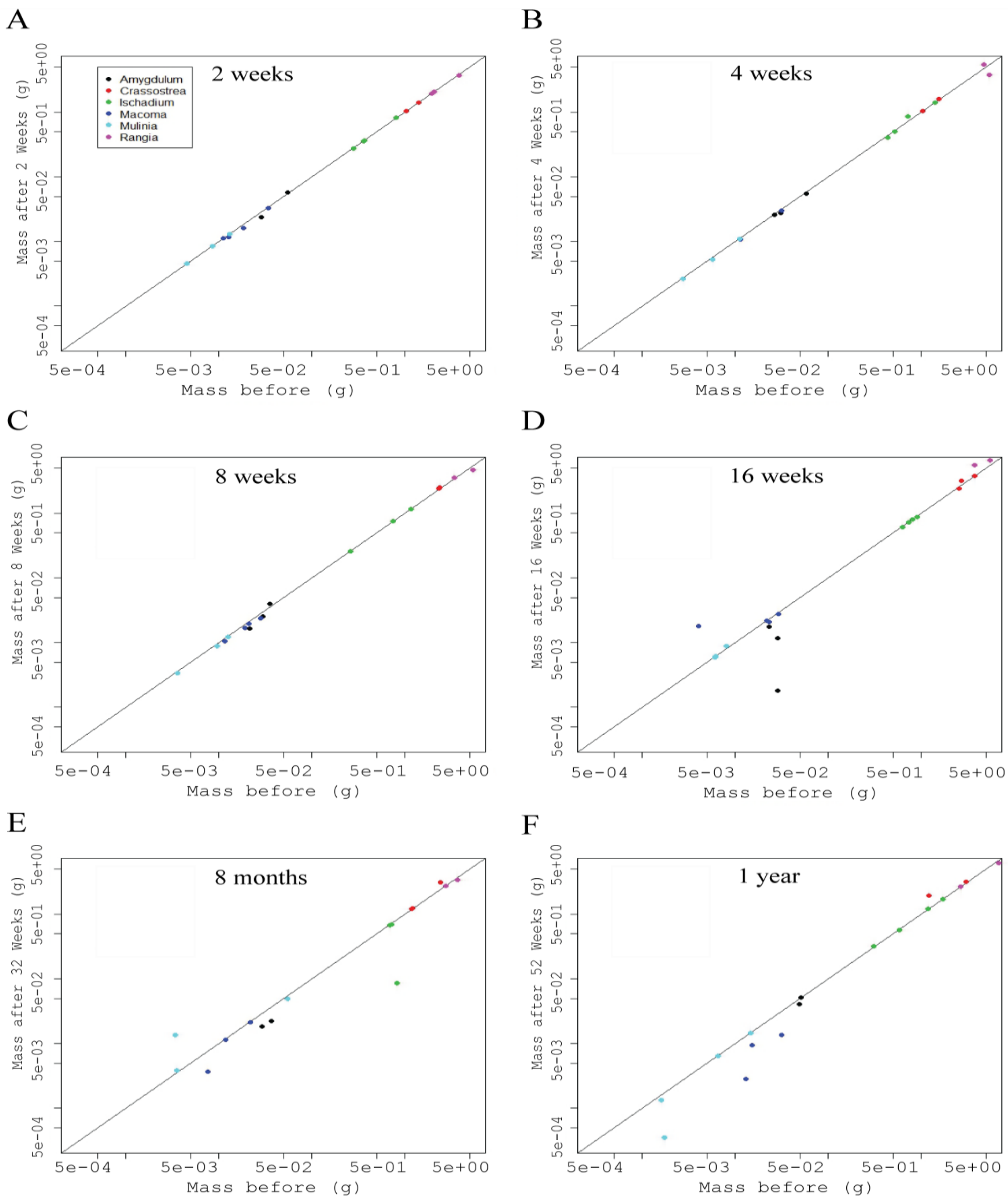

Figure 8, Plots of the masses of shells before and after deployment. A, 2 weeks; B, 4 weeks; C, 8 weeks; D, 16 weeks; E, 8 months; F, 1 year. Line of slope = 1 and intercept = 0 indicates no change in a specimen's mass.

In addition, an analysis of variance test was performed to test if percent change in shell masses differed among species. Percent change was chosen because of the difference in shell sizes and weights – i.e., a loss of 1 mg has a significant impact on the smaller shells as opposed to the larger shells. The F-test resulted in an F-value of 0.6652 (Df = 6, Pr(>F) = 0.6779), indicating that different species did not lose statistically different percentage of mass through the duration of the experiment.

A two-way analysis of variance test combining post-mortem age by species identity was also performed (Table 2). The result indicates that species identity is a more influential factor in determining change in mass in the experiment, but that neither factor is statistically significant.

			1-way ANOVA		
	Df	Sum Sq	Mean Sq	F value	Pr(>F)
species	6	10588	1764.7	0.6652	0.6779
			1-way ANOVA		
weeks	5	7104	1420.8	0.5338	0.7502
			2-way ANOVA		
species	6	10588	1764.7	0.6489	0.6909
weeks	5	7136	1427.2	0.5248	0.757

Table 2, ANOVA tests. 1-way ANOVA test results of percent change among species, 1-way ANOVA test results of percent change among collection time groups (weeks), 2-way ANOVA test results of percent change among species and collection time groups (weeks).

4. DISCUSSION

Abrasion patterns are a ubiquitous feature of shells that were deployed in Aransas Bay. The amount of abrasion that covers the shell increased over time resulting in exposure of the inner crystalline structure. Several *Amygdulum* and *Rangia* shells had exposed patches of inner crystalline structure on the exterior of the shell that appear to be associated with peeling and/or chipping of outer layers of the shell rather than abrasion.

Smaller shells lost weight due to several factors. They were thinner and more fragile than larger shells and therefore more likely to break during deployment. For example, after four weeks, all the *Amygdulum* shells were broken. *Macoma*, which also have thin, delicate shells, but of a cross-lamellar microstructure, were broken after a year in the field. Another important feature was the durability of the periostracum. Many times after a shell was broken, the periostracum would hold the large pieces of the shell together. Of the small shells, *Mulinia*, which has a small, sturdy shell that is thick for its size, lost the least proportion of mass per shell. This played a large role in the shell staying in one piece, for the most part, as opposed to *Macoma* and *Amygdulum*, the other small shells, most of which were broken into pieces.

Larger shells proved to be much more durable. With the exception of one *Ischadium* shell and two *Rangia* shells, all the large shells either stayed about the same mass or even gained mass. The mass gain was due to biological encrustation onto the interior or exterior of the shell, which had the effect of not only adding mass to the shells, but also shielding the shell from physical or chemical damage.

Size also played a role in the likelihood that a shell would be encrusted. All but five of the fifty larger shells had some sort of biological encrustation. Encrustation was a ubiquitous feature on the exterior of the *Ischadium* shells, and although all of these encrustations occurred while the animal was alive, they nonetheless helped to keep the shell preserved after death. *Crassostrea* and *Ischadium* are also epifaunal. It could be that encrusting organisms are adapted to the exterior of these shells and find them preferential to attach to. It could also be that when the epifaunal bivalve species used in the experiment die they are more likely to be exposed on the surface and have more encrustations.

Surprisingly, little or no evidence for chemical dissolution was detected in this experiment. That is not to say it did not occur. According to Berner (1981), marine sediment porewaters can become acidic when hydrogen sulfide released during the microbial oxidation of organic matter by sulfate reduction comes into contact with oxygenated water. This redox reaction occurs at the sediment water interface and continues one or two centimeters into the sediment, below which the sediment porewaters become anoxic. Any chemical dissolution would almost certainly enhance physical abrasion and vice versa. This chemical-physical feedback could play a key role in determining how quickly a shell degrades and explain why little evidence for chemical dissolution was found in this experiment. Chemical dissolution could have occurred before the abrasion and weakened the exterior and enabled physical abrasion to be the more evident form of alteration.

Temperature, salinity, sediment influx, dissolved nutrients, and dissolved oxygen all make contributions that impact coastal and estuarine environments. These environmental factors change seasonally and influence preservation. A yearly taphonomic cycle could provide a reason for some of the variation seen in shell alterations. When the shells were deployed in late summer, the water column had become stratified (DiMarco et al. 2012; Ritter and Montagna, 1999; Montagna and Ritter, 2006). This meant dissolved nutrients and dissolved oxygen could not circulate freely throughout the water column. This, in turn, limited chemical, physical, and biological alterations to the shells. In the fall, the thermocline, which stratified the water column in the summer, weakens and allows the water column to mix. Biological, chemical, and physical activity is encouraged during this time. In winter, the thermocline strengthens and inhibits biological, chemical, and physical alterations to the shell. Vertical mixing of nutrients in the water column, from a weakened thermocline, in the spring and early summer sparks biological activity. Eight-month and one-year shells had a higher proportion of cemented sediment grains, and larger shells had more encrustations compared to earlier shells. This indicates that the spring and early summer support greater chemical and biological activity that affects post-mortem alterations of shells.

Factors such as size and thickness influence the likelihood a shell will fragment and become encrusted. Kosnik et al. (2009) concluded factors such as size, thickness, and density were the determining characteristics in a shell's preservability, and this study confirms this conclusion. However, the importance of tapho-depositional features, such as frequency of sediment reworking, net rate of sedimentation, and porewater chemistry as the main determinants of preservation should not be ignored. For example, different environments have different carbonate budgets (Davies et al., 1989), meaning that dead shells accumulate at different rates in different environments. These tapho-depositional features will determine the common taphonomic pathway in a given depositional setting that is experienced by shells with contrasting sizes, thicknesses, and densities.

Cummins et al. (1986) concluded that taphonomic loss in Copano Bay happens at a measurable and predictable rate. According to their field-based measurements, some species had a post-mortem half-life not lasting longer than one year, while other species saw no discernible alteration. In this study, larger shells gained weight and smaller shells lost weight suggesting a preservation bias in favor of large shells. Cummins et al. (1986) also assumed that dissolution was the main reason for taphonomic loss. As SEM images show, however, the majority of the damage done to the shells in this experiment was caused by physical abrasion. Because this is the first study to perform field experiments to ascertain the nature of damage being done to shells during the initial stages of post-mortem alteration, it raises the question, "How much taphonomic loss is being assumed as dissolution, when it may well be abrasion?"

5. CONCLUSIONS

Physical abrasion was the dominant form of degradation observed in a series of field-deployed shell fragments. It has previously been proposed that carbonate loss in muddy marine settings is ultimately due to dissolution. This experiment demonstrates the need for loss rates to be measured empirically, not simply assumed based on expected dissolution rates. Measurements showed smaller shells losing mass and larger shells gaining mass demonstrating a clear preservation bias towards larger shells. One of the reasons why larger shells gained mass during the experiment was due to encrusting organisms that attached themselves to the shells. These encrustations acted as armor to preserve the large shells from chemical and physical alteration. Microstructure or chemical makeup of a shell appears to be less influential than size, thickness, and density.

REFERENCES

Behrensmeyer, A.K., Fursich, F.T., Gastaldo, R.A., Kidwell, S.M., Kosnik, M.A., Kowalewski, M., Plotnick, R.E., Rogers, R.R., Alroy, J. 2005. Are the most durable shelly taxa also the most common in the marine fossil record? Paleobiology, v. 31, p. 607-623.

Berner, R.A. 1981. A new geochemical classification of sedimentary environments. Journal of Sedimentary Pretrology, v. 51, p. 359-365.

Callender, W.R., Staff, G.M., Parsons-Hubbard, K.M., Powell, E.N., Rowe, G.T., Walker, S.E., Brett, C.E., Raymond, A., Carlson, D.D., White, S., Heise, E.A., 2002. Taphonomic trends along a forereef slope: Lee Stocking Island, Bahamas. I. Location and water depth. Palaios, v. 17, p. 50-65.

Carroll, M., Kowalewski, M., Simoes, M.G., Goodfriend, G.A., 2003. Quantitative estimates of time-averaging in terebratulid brachiopod shell accumulations from a modern tropical shelf. Paleobiology, v. 29, p. 381-402.

Cummins, H., Powell, E.N., Stanton Jr., R.J., Staff, G., 1986. The rate of taphonomic loss in modern benthic habitats: How much of the potentially preservable community is preserved? Palaeogeography, Palaeoclimatology, Palaeoecology, v.52, p. 291-320.

Davies, D. J., Powell, E. N. Stanton, R. J., Jr. 1989. Relative rates of shell dissolution and net sediment accumulation - a commentary: Can shell beds form by the gradual accumulation of biogenic debris on the sea floor? Lethaia, v. 22, p. 207-212.

Dimarco, S.F., Strauss, J., May, N., Mullins-Perry, R.L., Grossman, E.L., Shormann, D. 2012. Texas coastal hypoxia linked to Brazos River discharge as revealed by oxygen isotopes. Aquatic Geochemistry, v. 18, p. 159–181.

Flessa, K.W., Kowalewski, M., 1994. Shell survival and time-averaging in nearshore and shelf environments: estimates from the radiocarbon literature. Lethaia, v. 27, p. 153-165.

Kidwell, S.M., Brenchley, P.J., 1994. Patterns in bioclastic accumulation through the Phanerozoic: Changes in input or destruction? Geology, v. 22, p. 1139-1143.

Kidwell, S.M., 2001. Preservation of species abundance in marine death assemblages. Science, v. 294, p. 1091-1094.

Kidwell, S.M., 2002. Time-averaged molluscan death assemblages: Palimpsests of richness,snapshots of abundance. Geology, v. 30, p. 803-806.

Kosnik, M.A., Hua, Q., Kaufman, D.S., Wust, R.A., 2009. Taphonomic bias and time-averaging in tropical molluscan death assemblages: Differential shell half-lives in Great Barrier Reef sediment. Paleobiology, v. 35, p. 565-586.

Krause Jr., R.A., Barbour, S.L., Kowalewski, M., Kaufman, D.S., Romanek, C.S., Simoes, M.G., Wehmiller, J.F., 2010. Quantitative comparisons and models of time-averaging in bivalve and brachiopod shell accumulations. Paleobiology, v. 36, p. 428-452.

Miller, A.I., 1988. Spatial resolution in subfossil molluscan remains: Implications for paleobiological analyses. Paleobiology, v. 14, p. 91-103.

Montagna, P. A., Ritter, C. 2006. Direct and indirect effects of hypoxia on benthos in

Corpus Christi Bay, Texas, USA. Journal of Experimental Marine Biology and Ecology, v. 330, p. 119–131.

Olszewski, T.D., 2004. Modeling the influence of taphonomic destruction, reworking, and burial on time-averaging in fossil accumulations. Palaios, v. 19, p. 39-50.

Peterson, C. H. 1976. Relative abundances of living and dead molluscs in two California lagoons. Lethaia, v. 9, p. 137-148.

Staff, G.M., Stanton, R.J., Jr., Powell, E.N. H. Cummins, 1986. Time-averaging, taphonomy and their impact on paleocommunity reconstruction: Death assemblages in Texas Bays. Geological Society of America Bulletin; 97:428-443.

Taylor, J.D., Kennedy, W.J., and Ritter, C. Montagna, P. A. 1999. Seasonal hypoxia and models of benthic response in a Texas bay. Estuaries, v. 22, p. 7–20.

Taylor, J.D., Kennedy, W.J., Hall, A. 1973, The shell structure and mineralogy of the Bivalvia, Part II, Lucinacea-Clavagellacea. Bull. Brit. Mus. (Nat. Hist.), Zool. v. 22, p. 253-294.

Warme, J. E. 1969. Live and dead molluscs in a coastal lagoon. Journal of Paleontology v. 43, p. 141-150

APPENDIX A

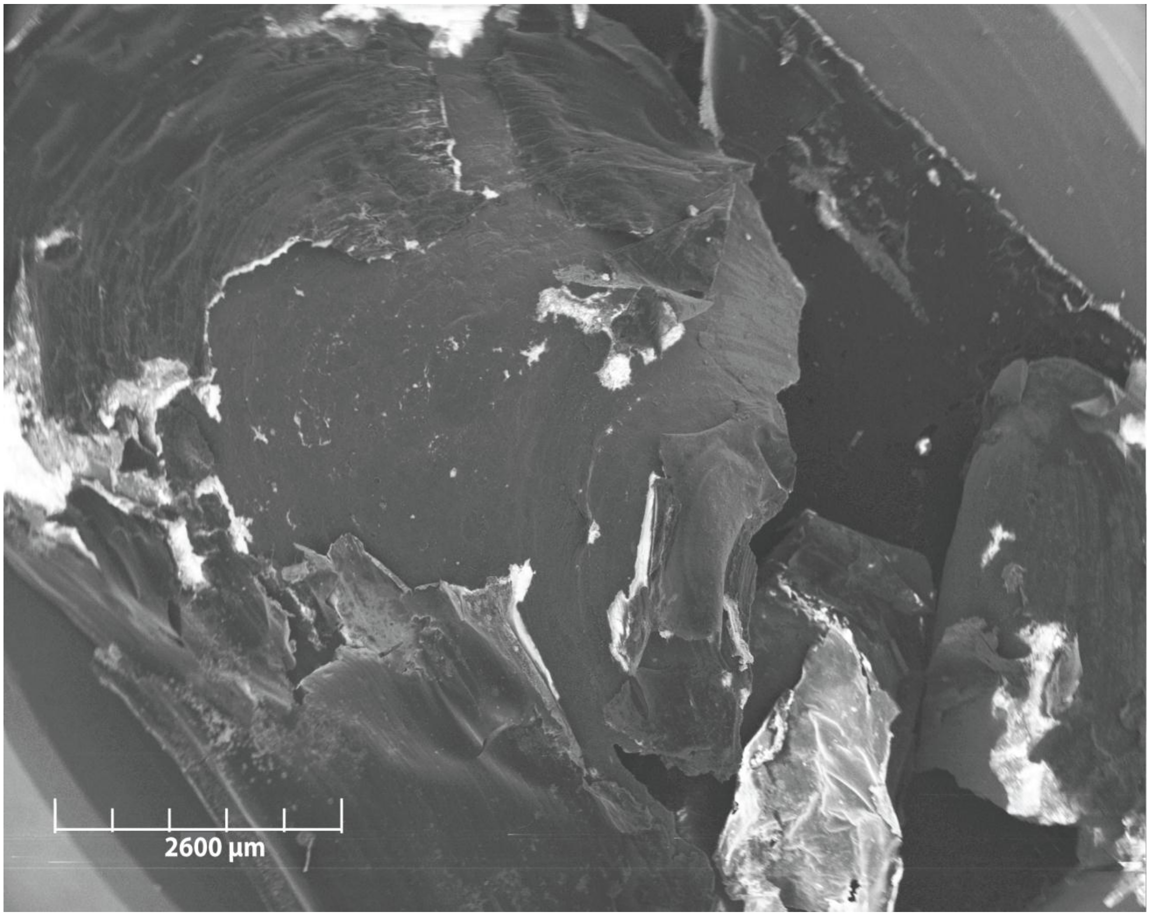

Figure A1, Amygdulum 2, 8 weeks

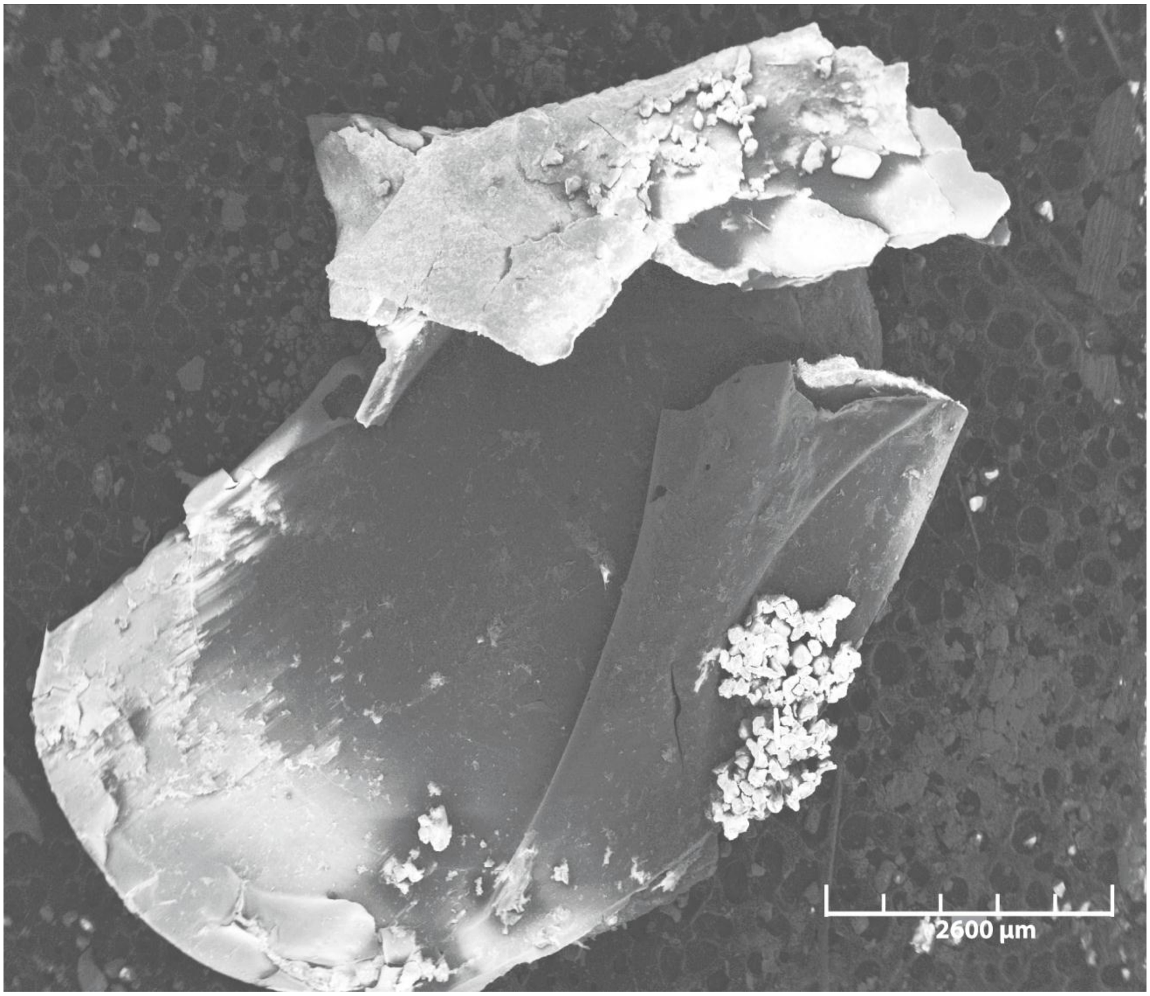

Figure A2, Amygdulum 3, 4 months

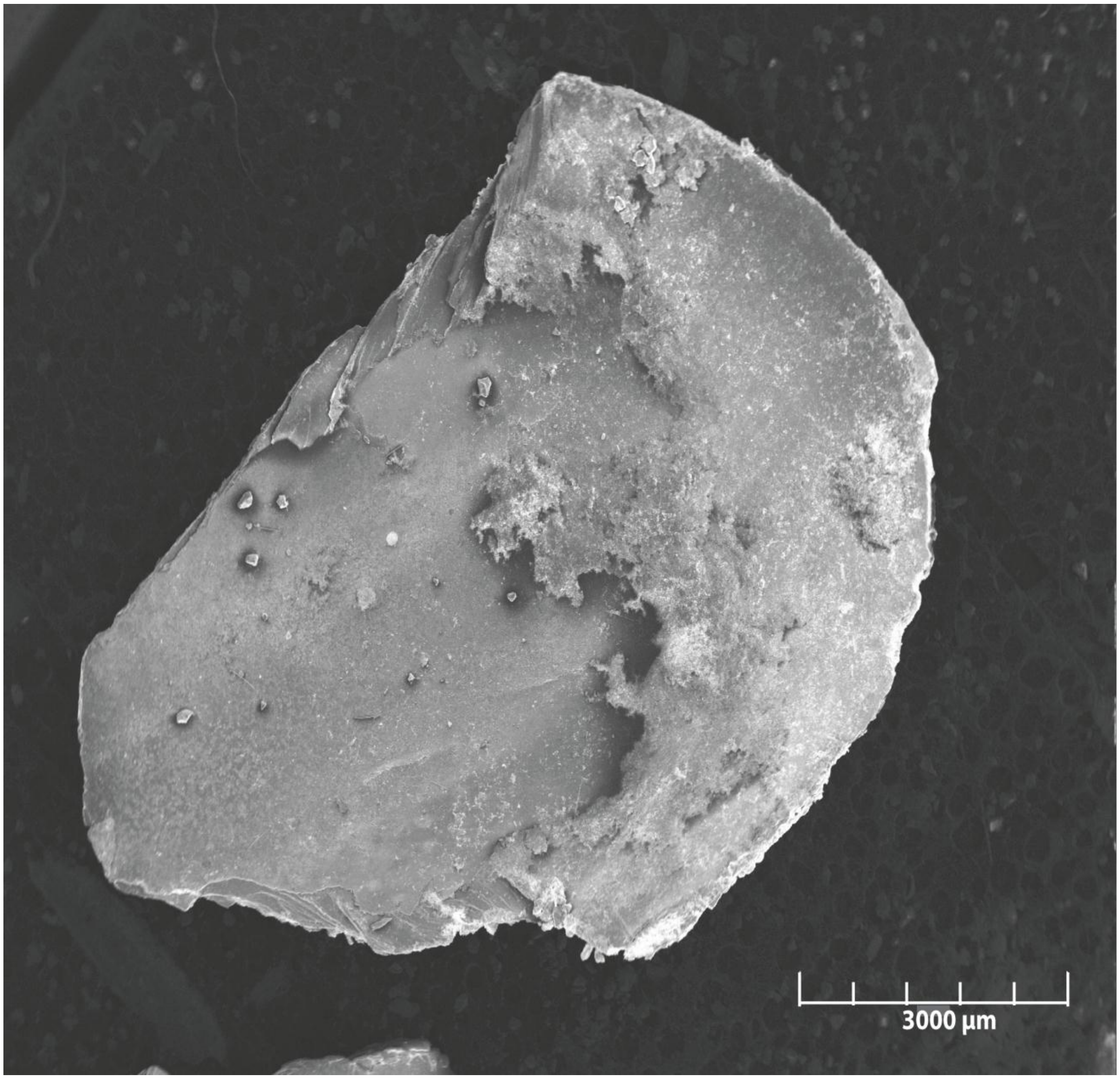

Figure A3, Amygdulum 5, 1 year

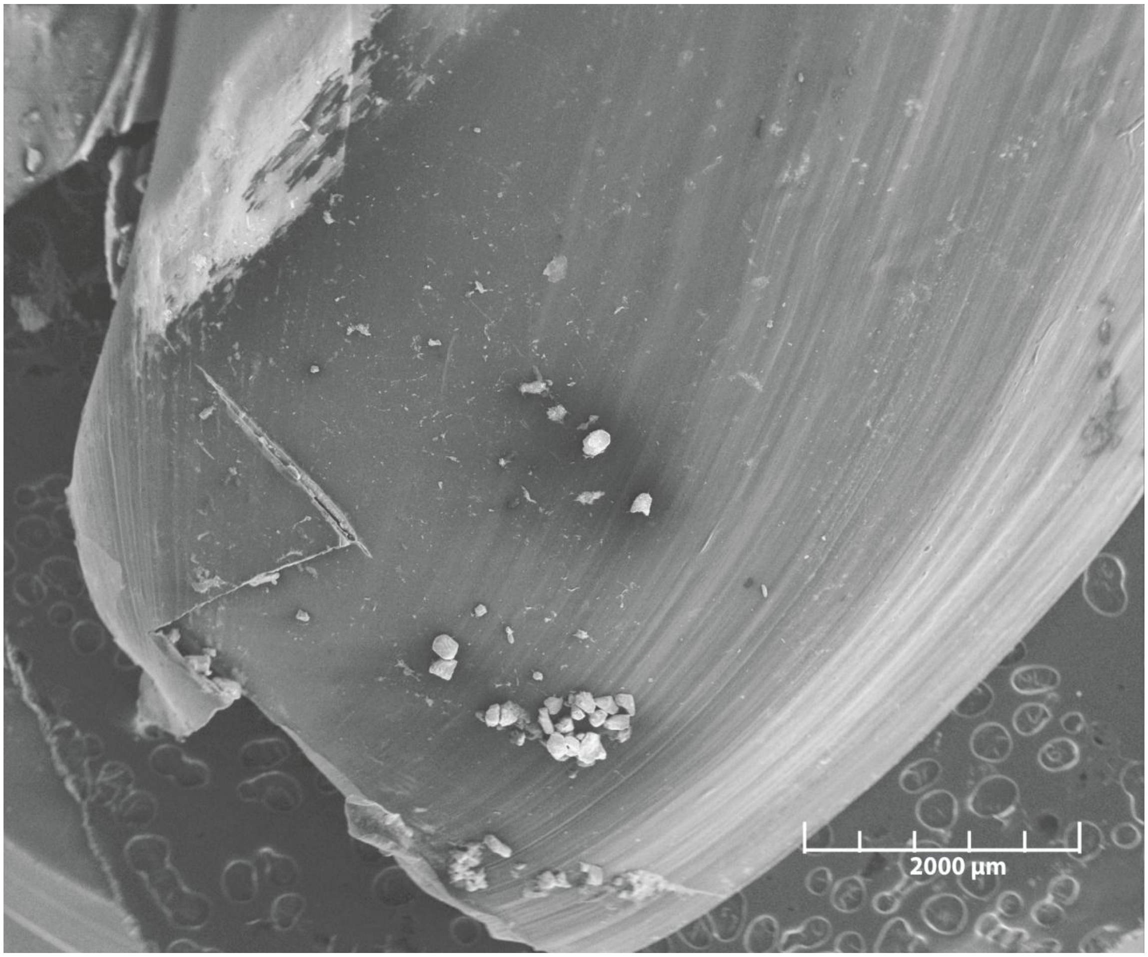

Figure A4, Amygdulum 9, 2 weeks

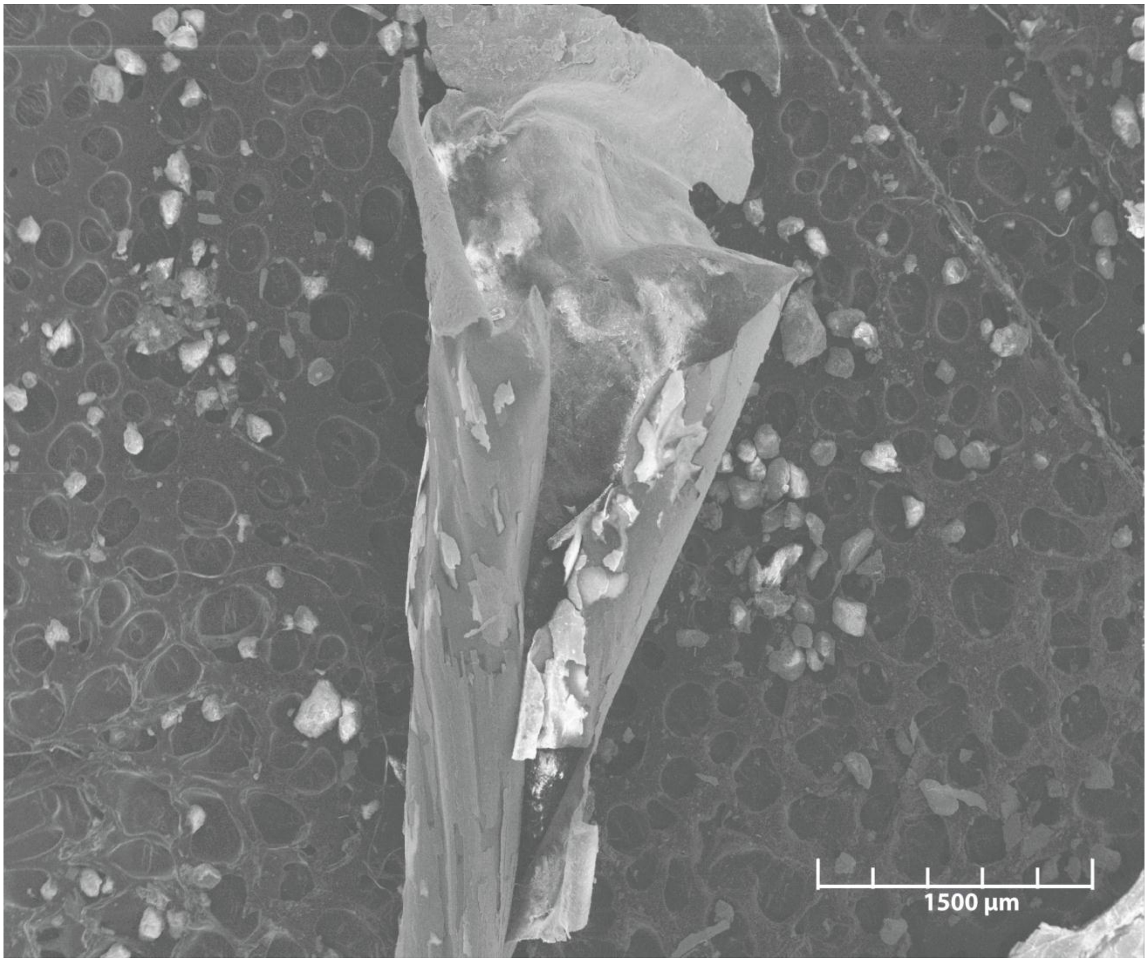

Figure A5, Amygdulum 10, 4 months

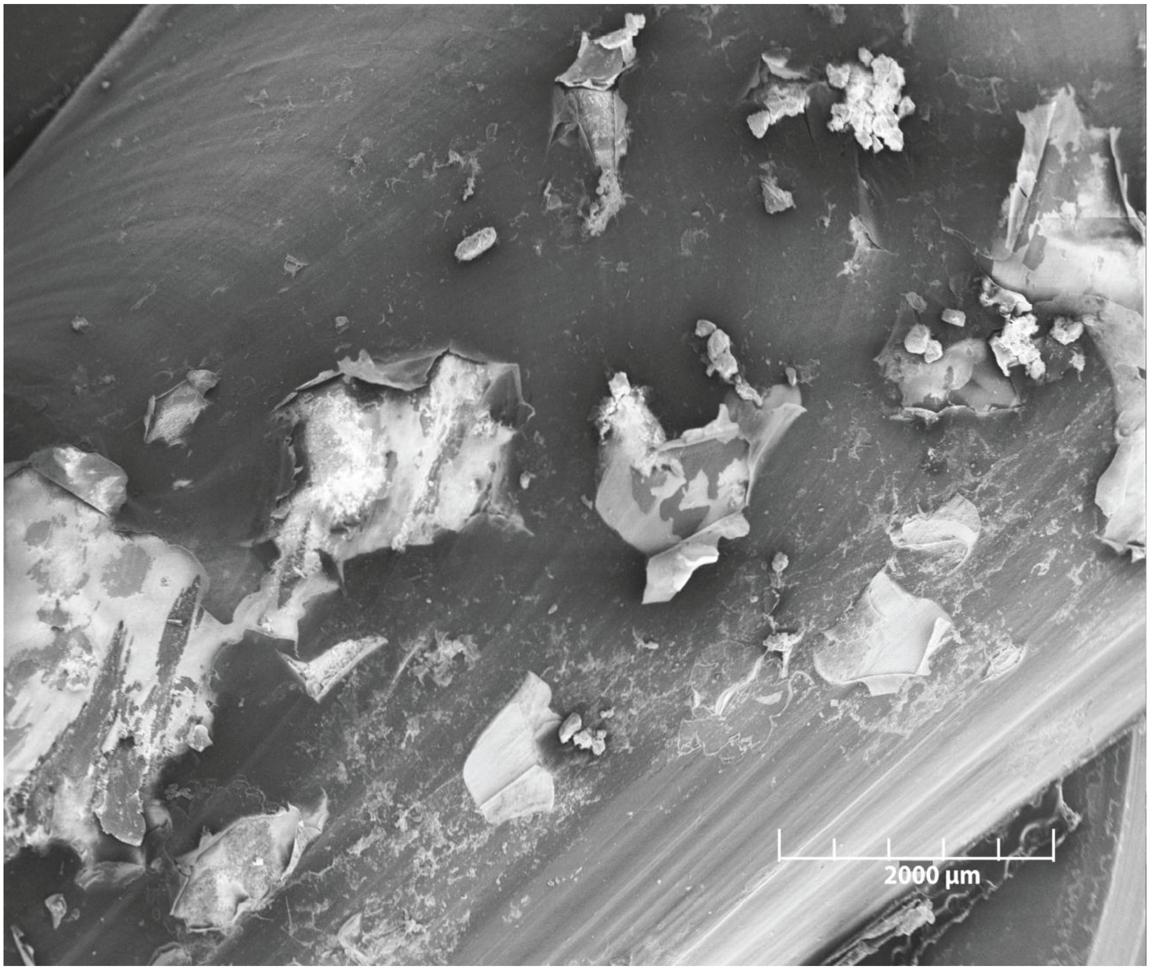

Figure A6, Amygdulum 11, 4 weeks

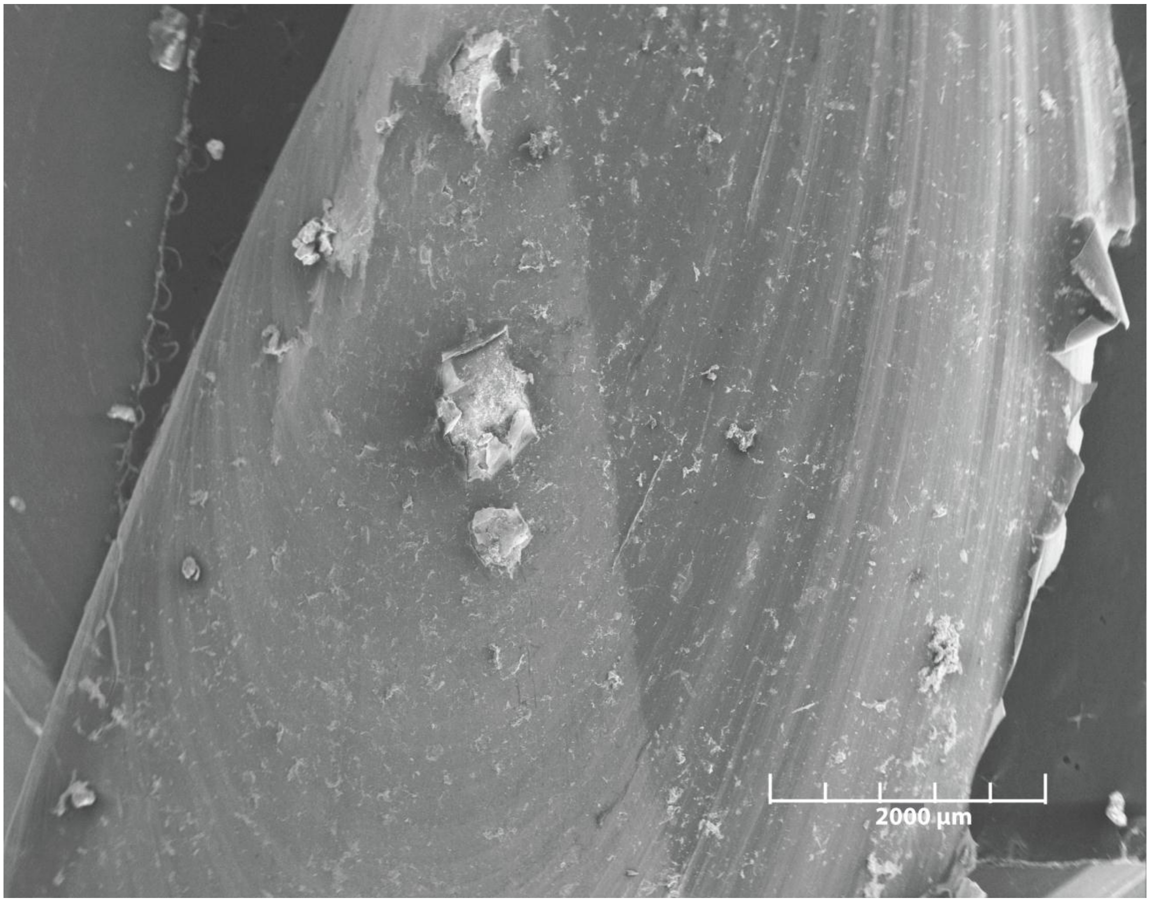

Figure A7, Amygdulum 12, 4 weeks

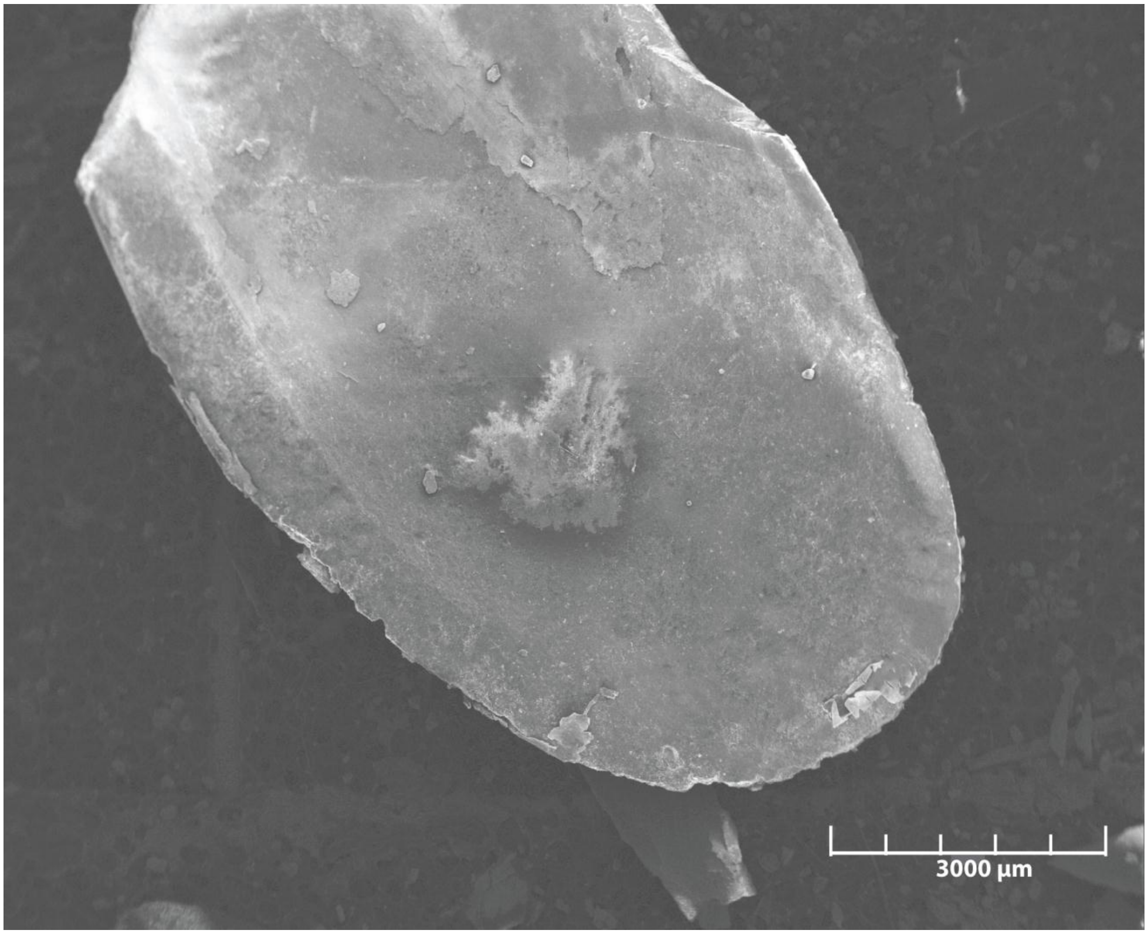

Figure A8, Amygdulum 13, 8 months

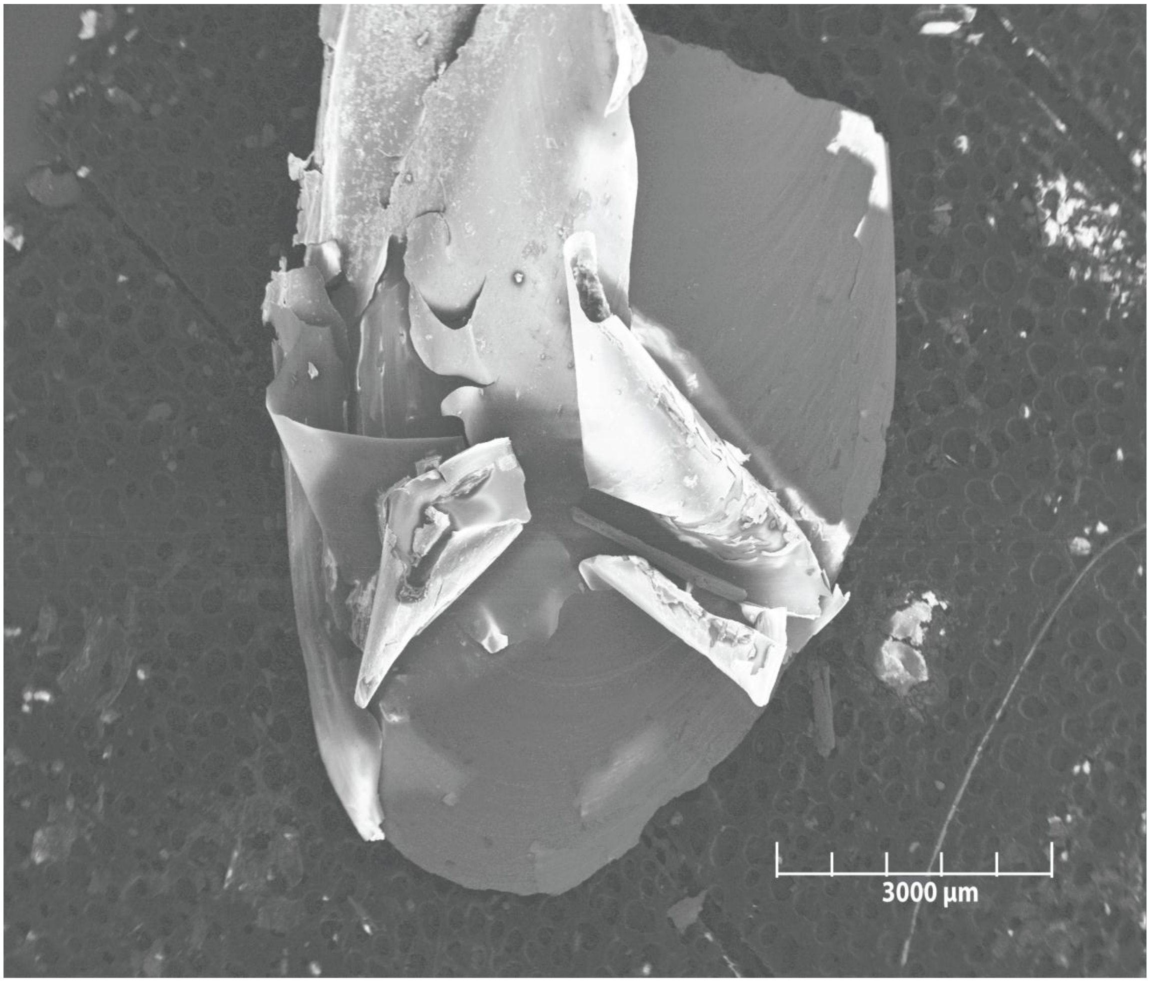

Figure A9, Amygdulum 15, 8 weeks

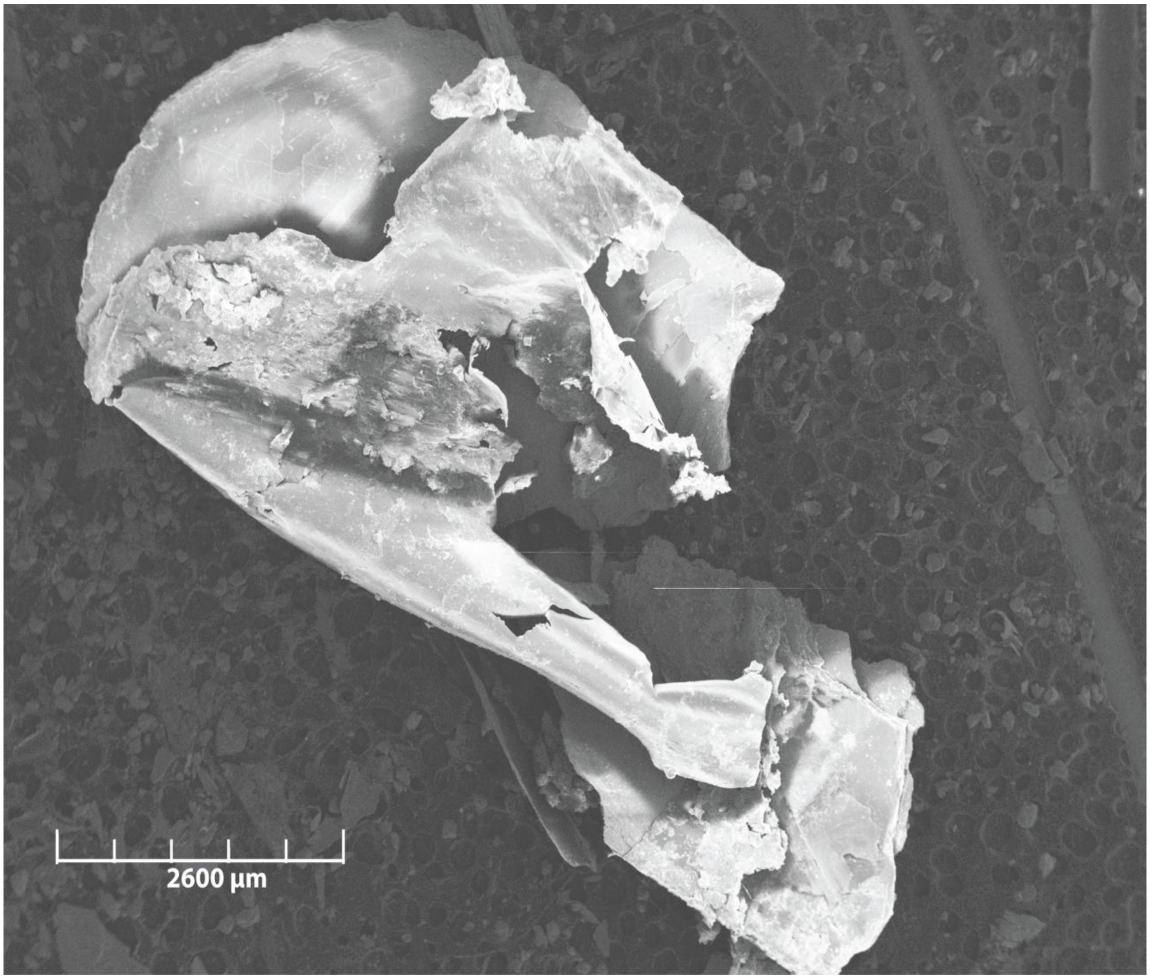

Figure A10, Amygdulum 17, 4 months

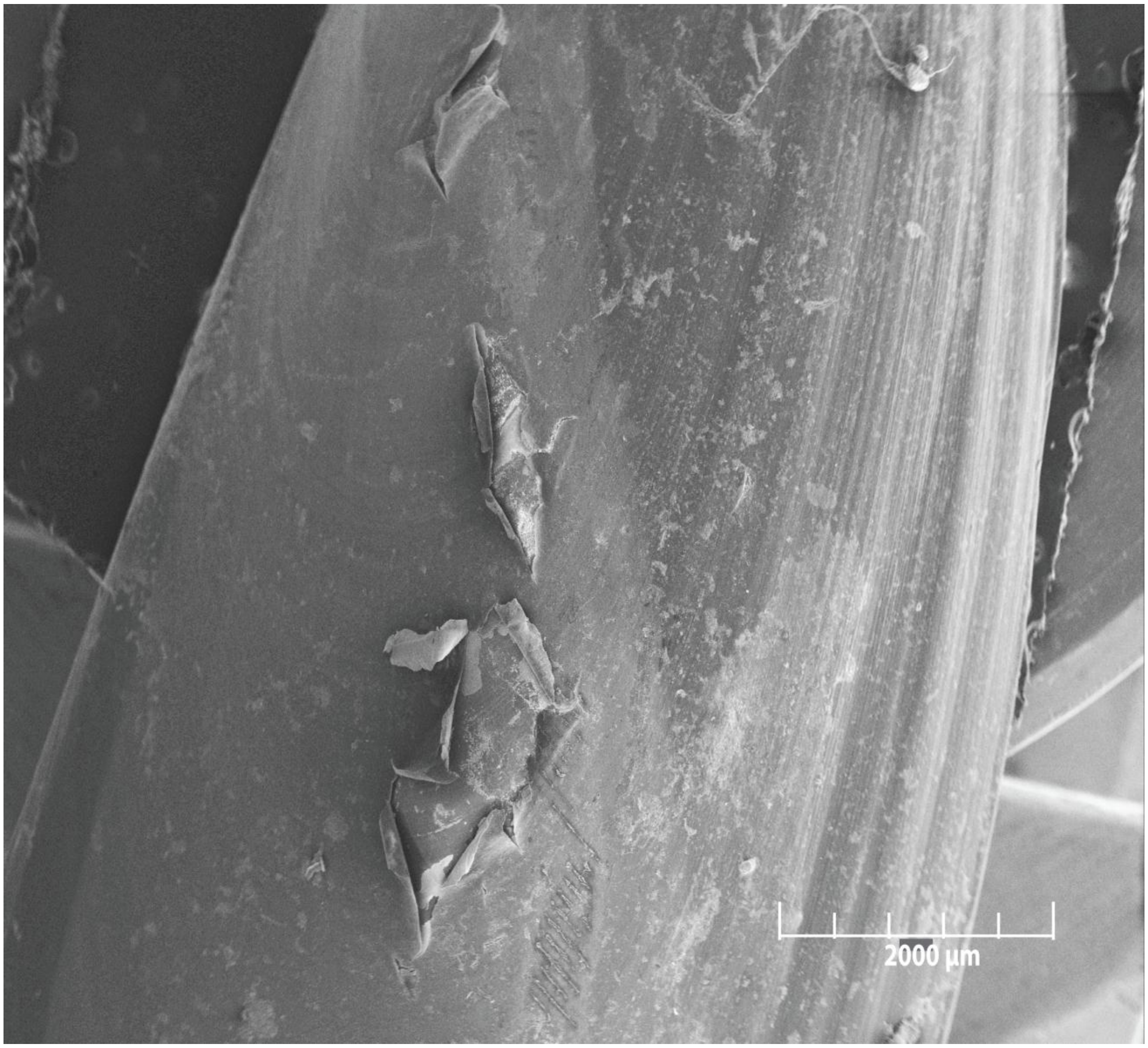

Figure A11, Amygdulum 18, 4 weeks

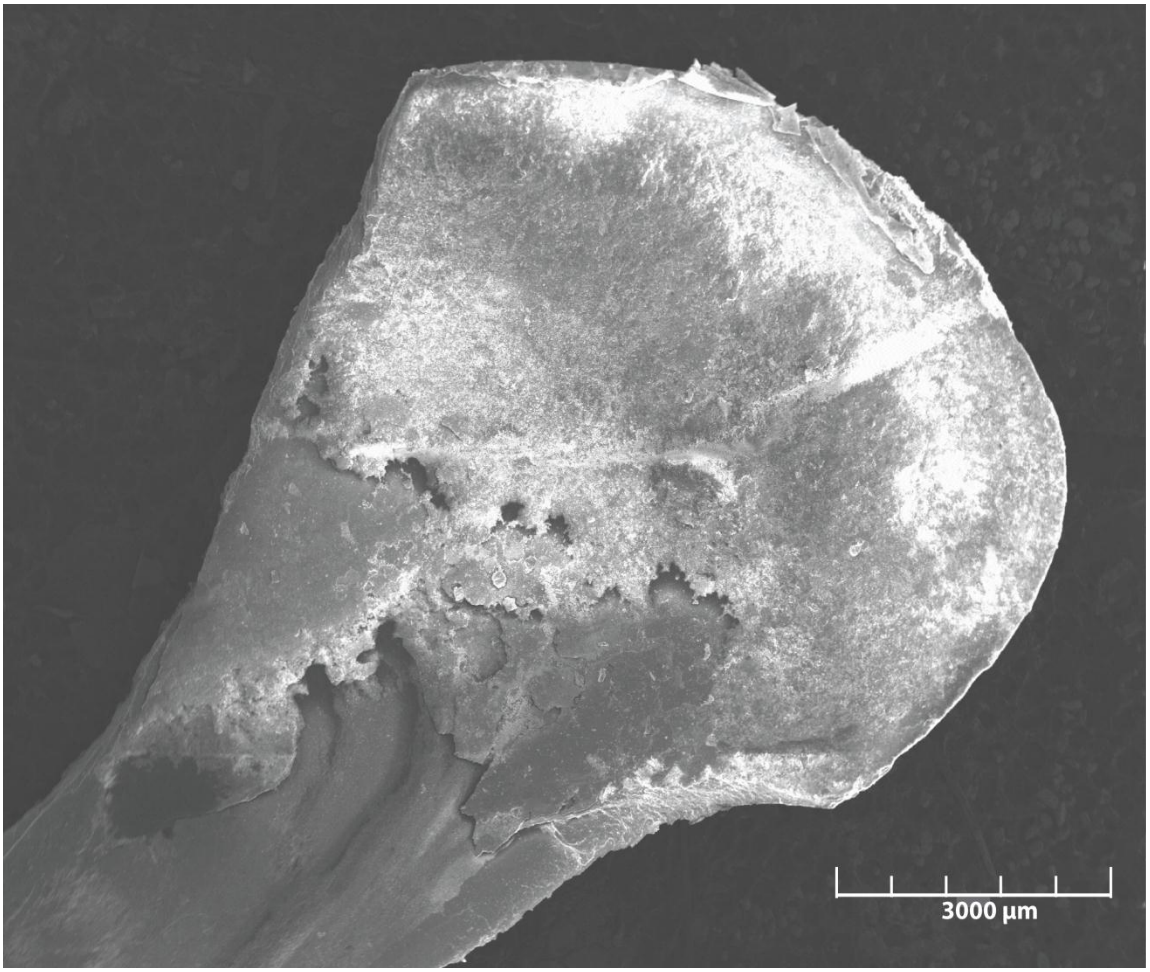

Figure A12, Amygdulum 20, 1 year

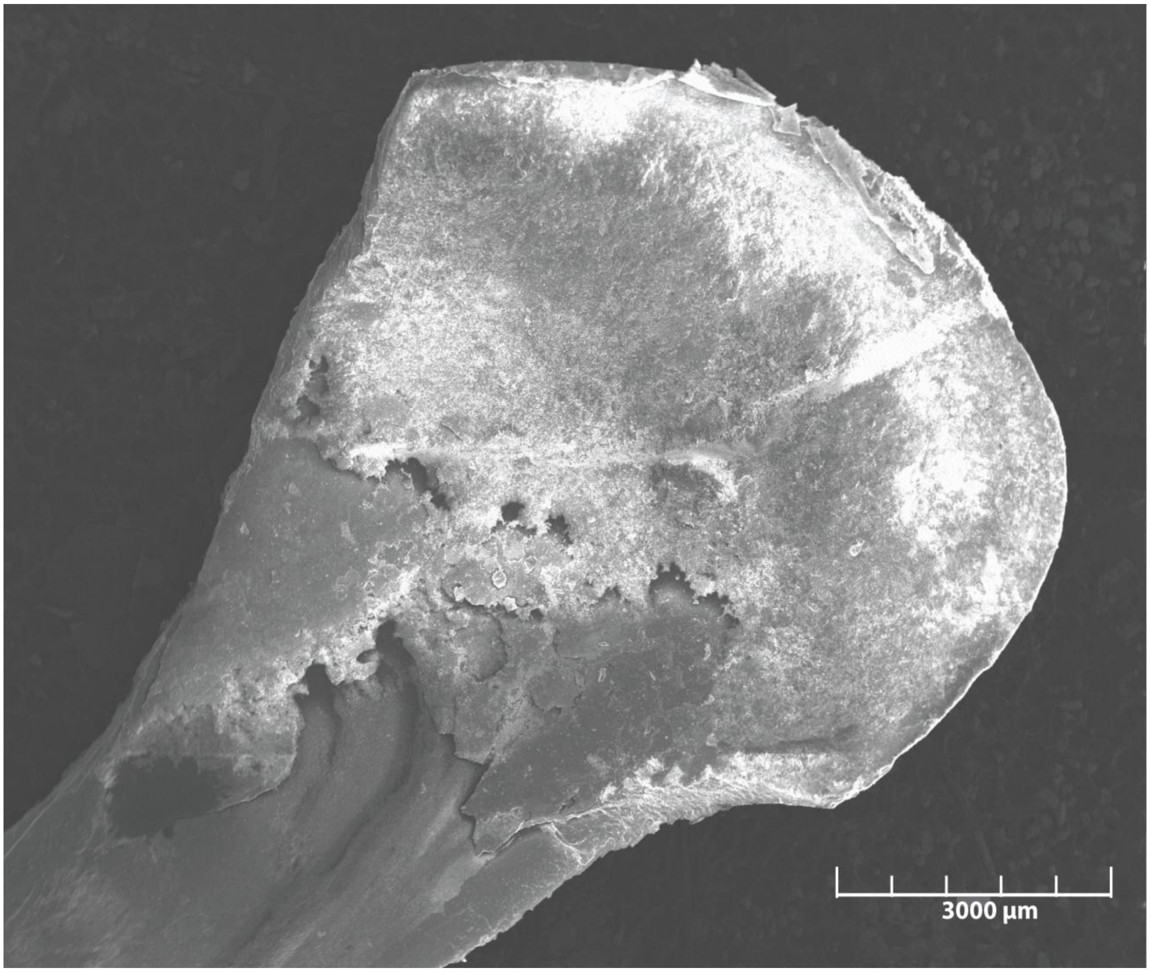

Figure A13, Amygdulum 20, 1 year

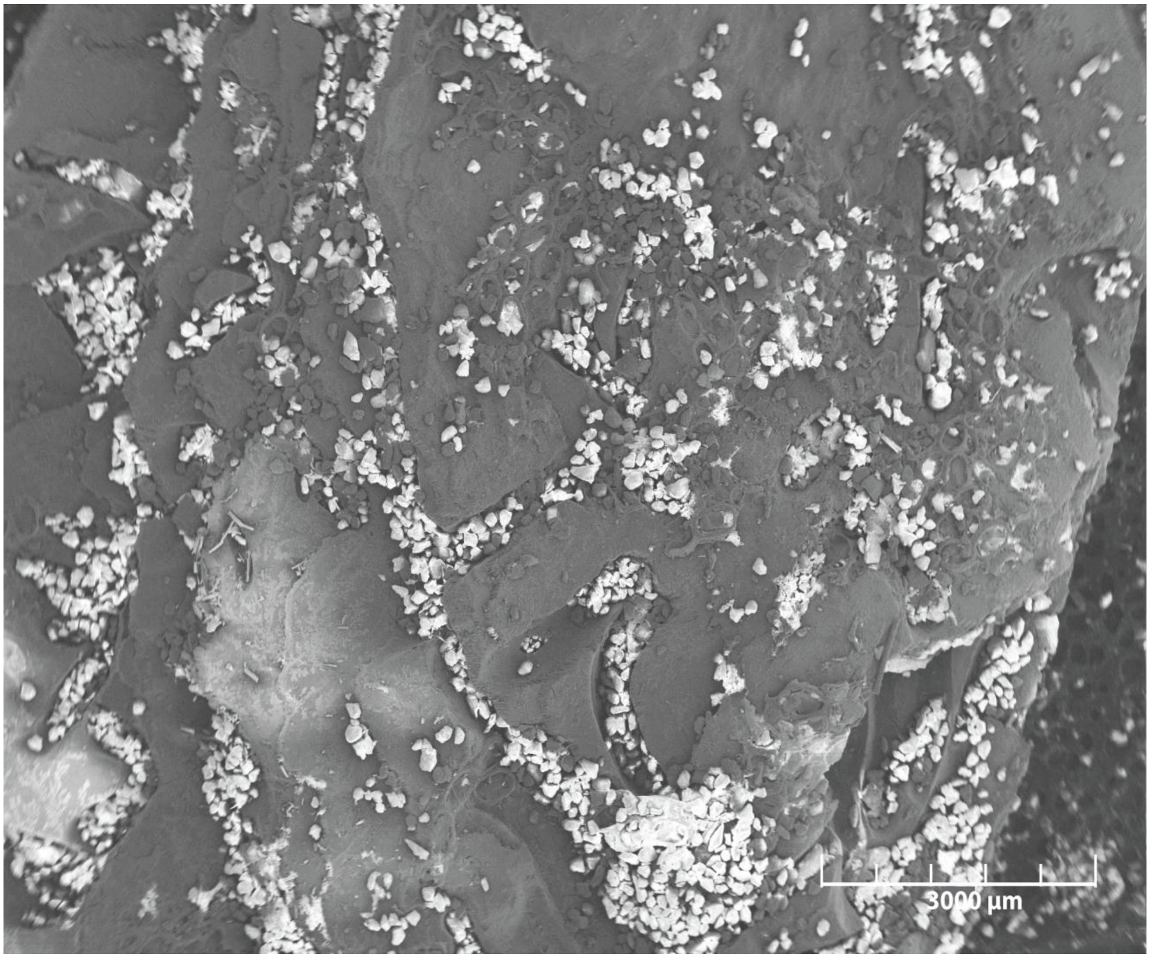

Figure A14, Crassostrea 2, 1 year

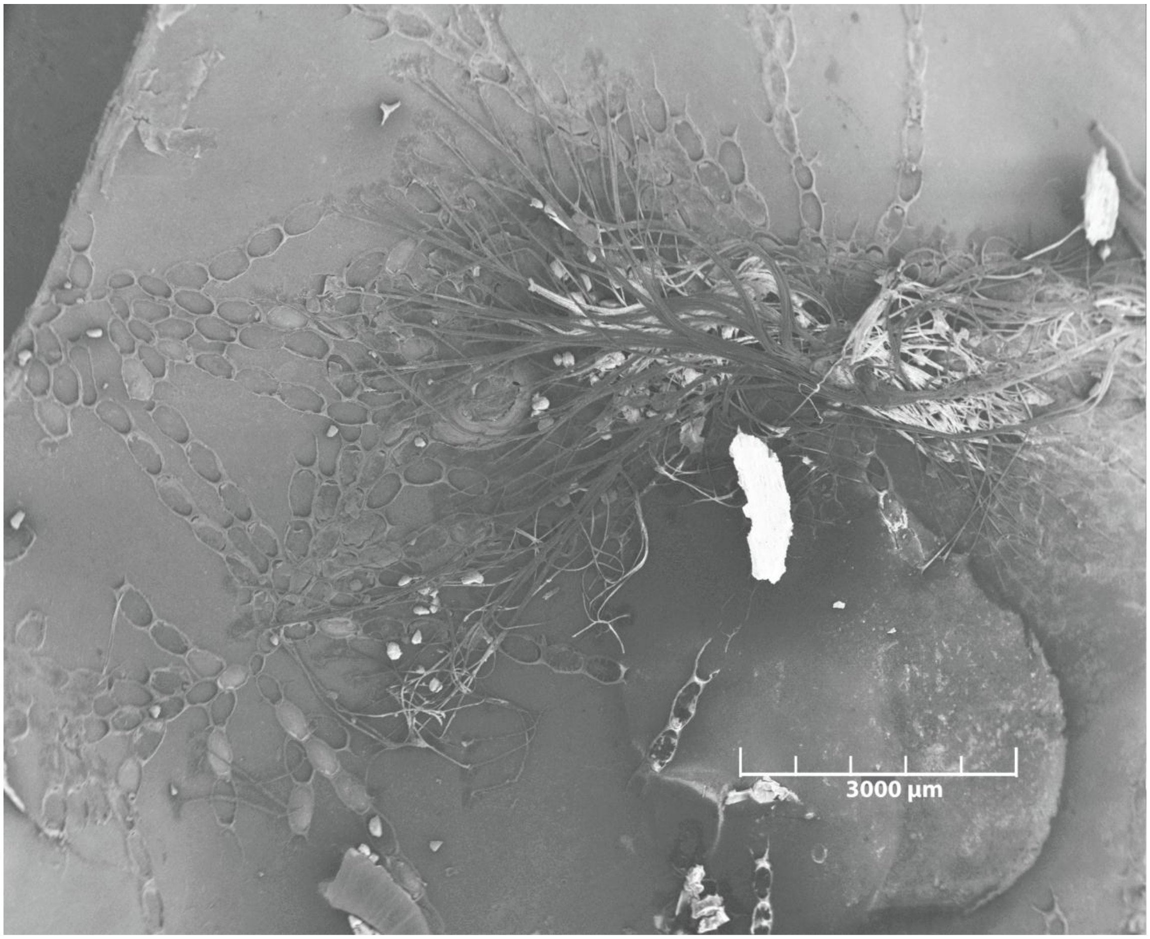

Figure A15, Crassostrea 2, 4 weeks

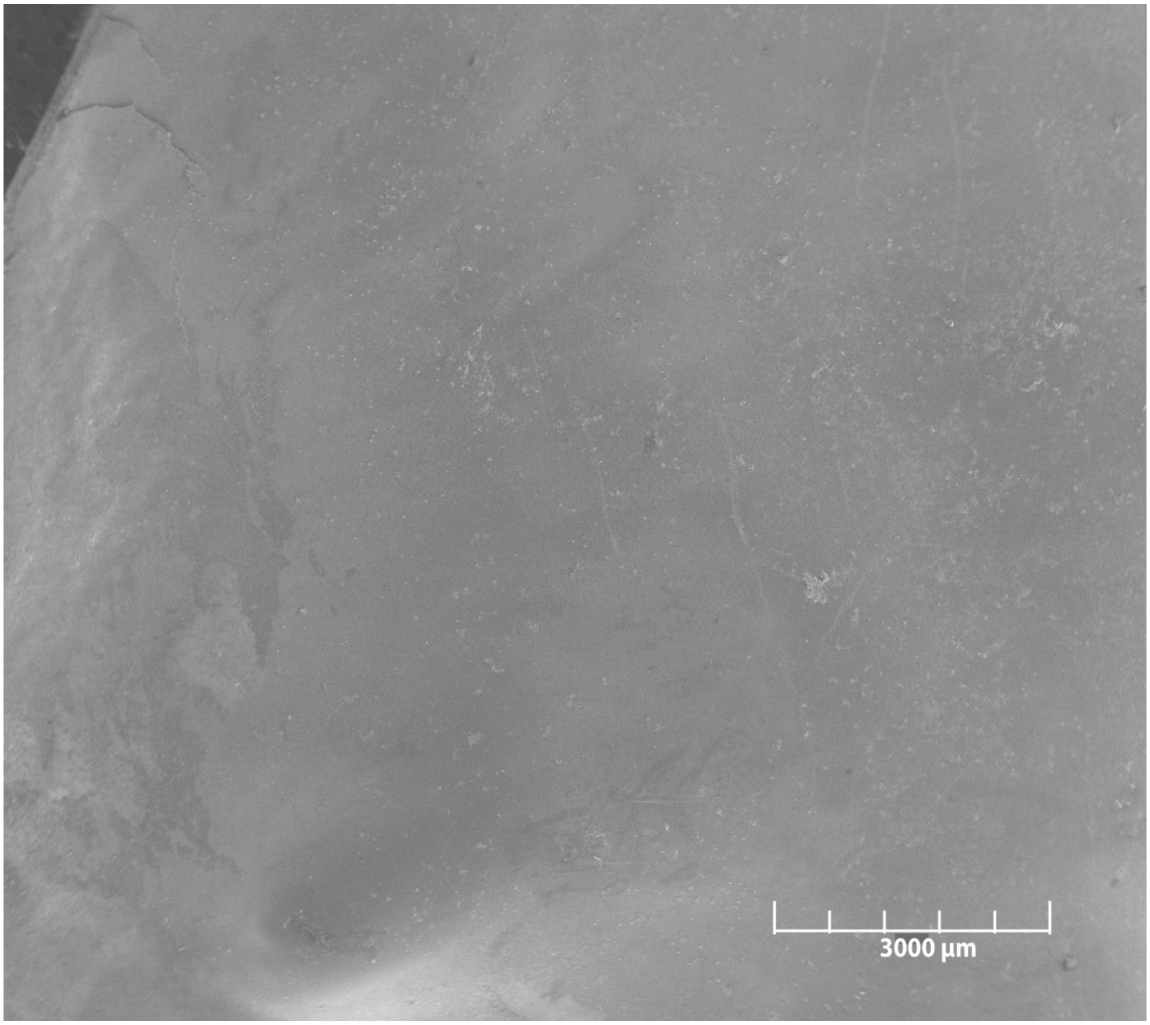

Figure A16, Crassostrea 3, 2 weeks

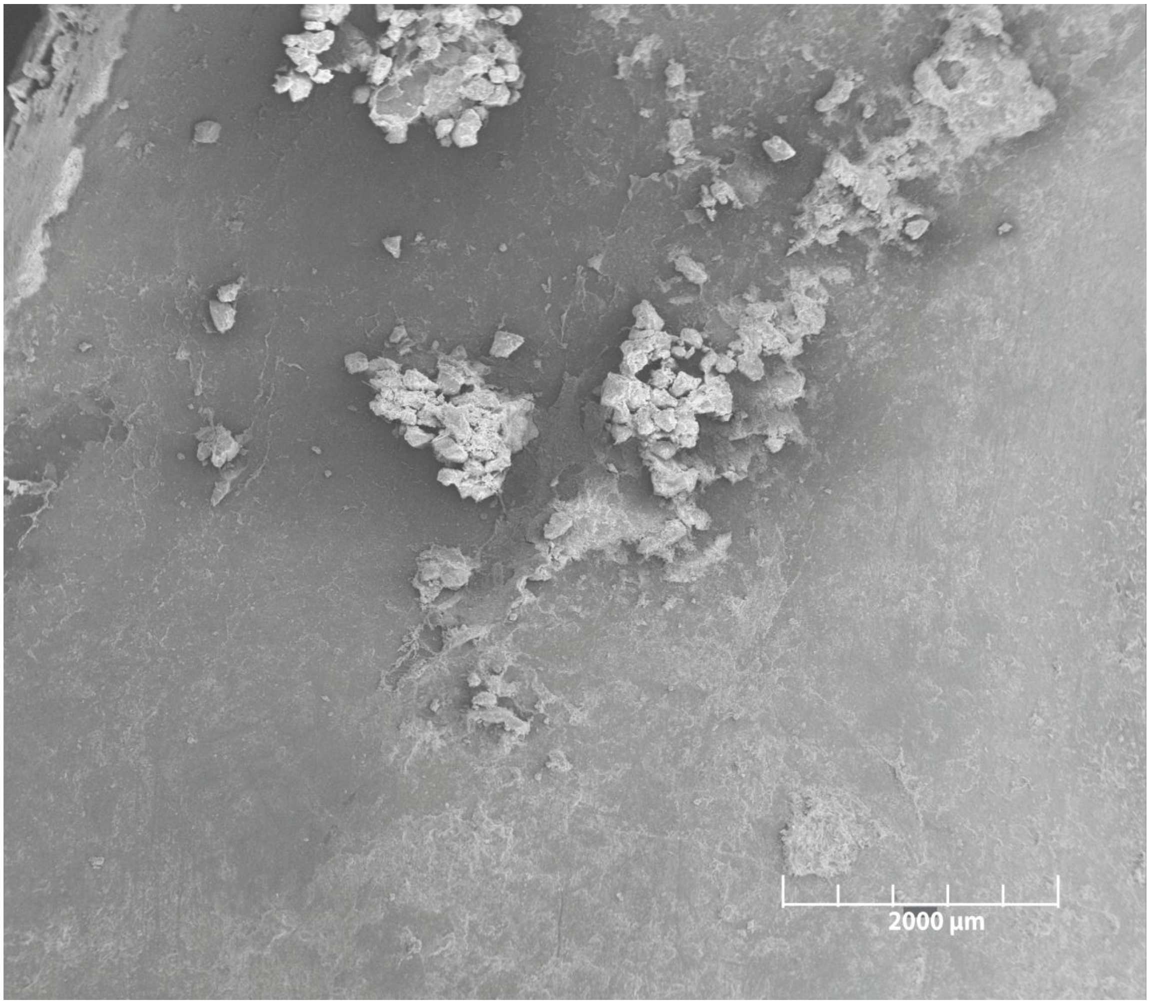

Figure A17, Crassostrea 5, 8 months

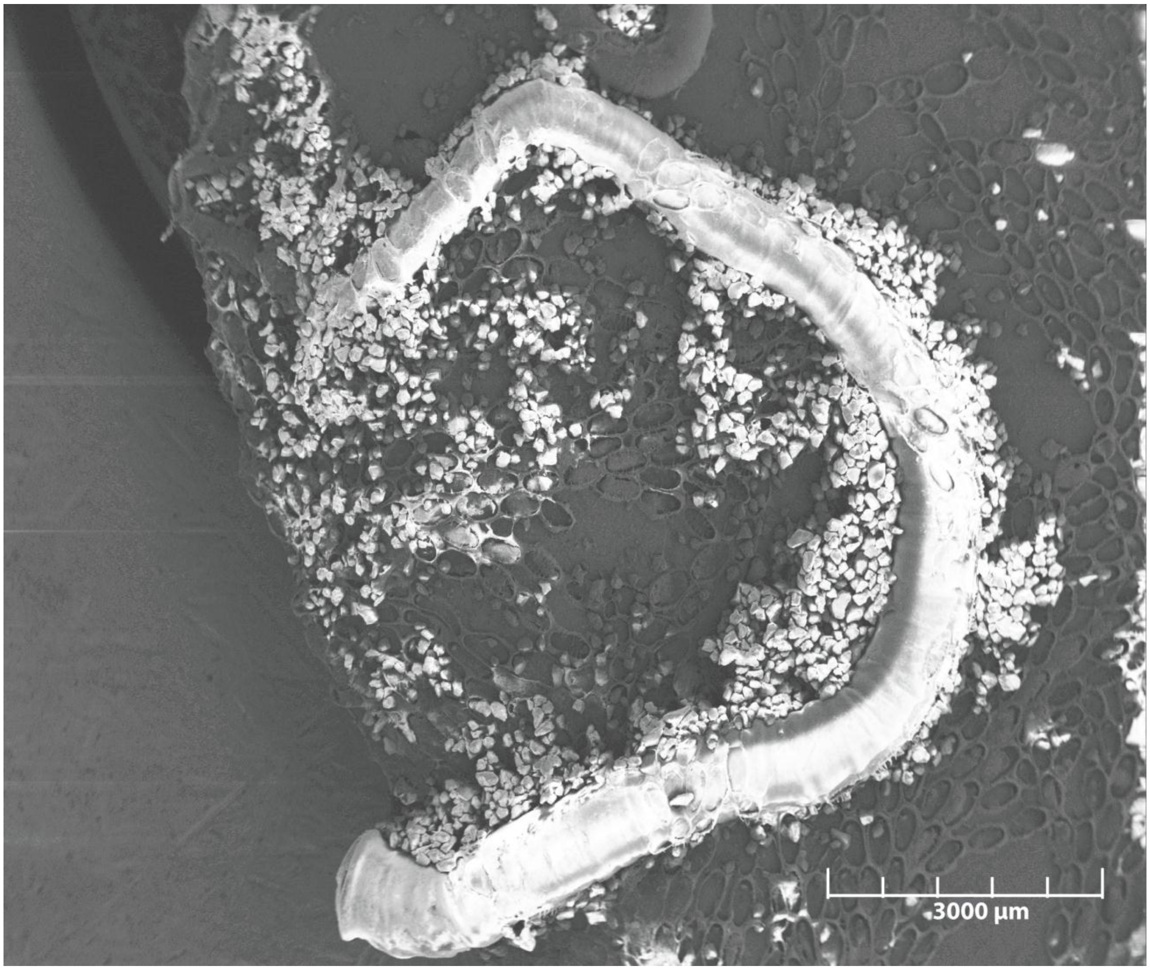

Figure A18, Crassostrea 5, 8 weeks

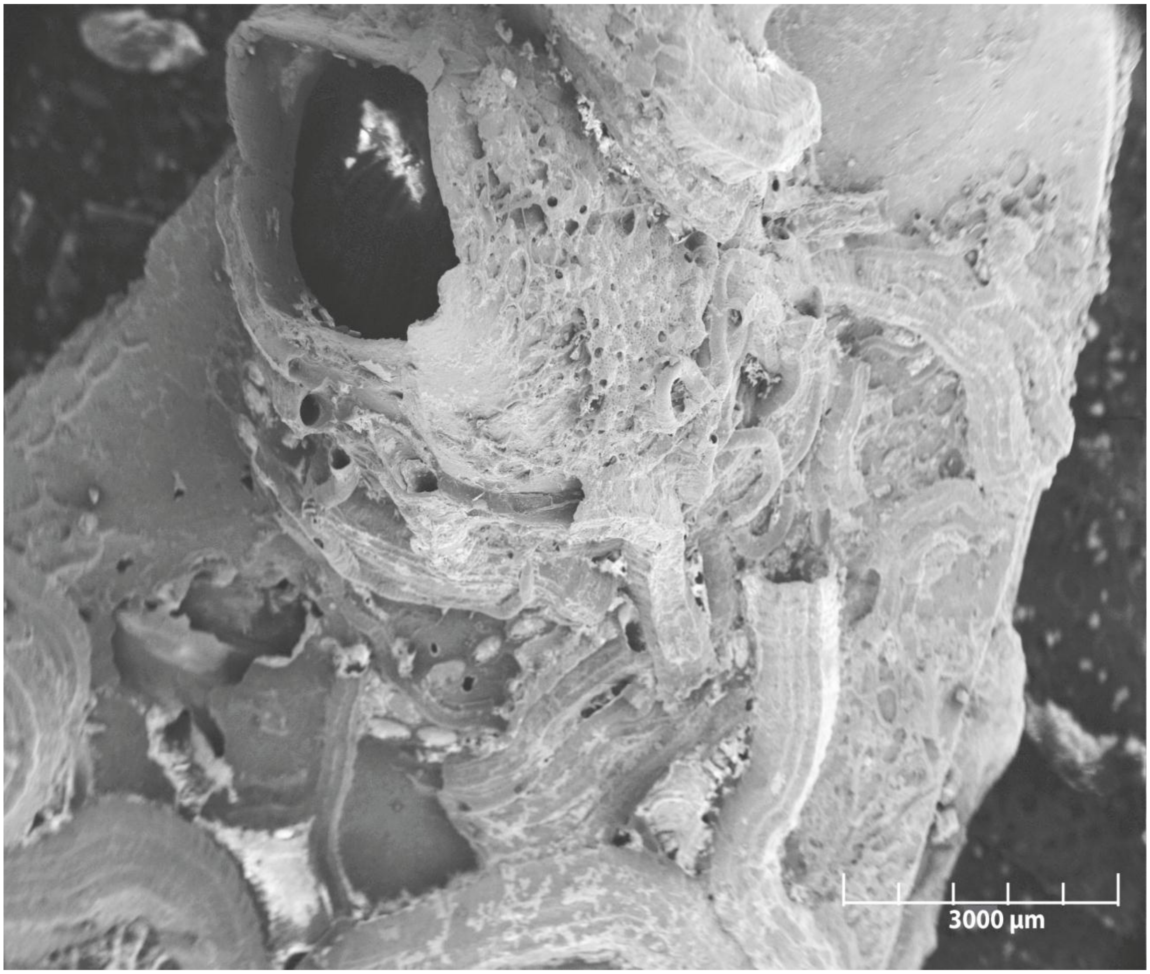

Figure A19, Crassostrea 6, 1 year

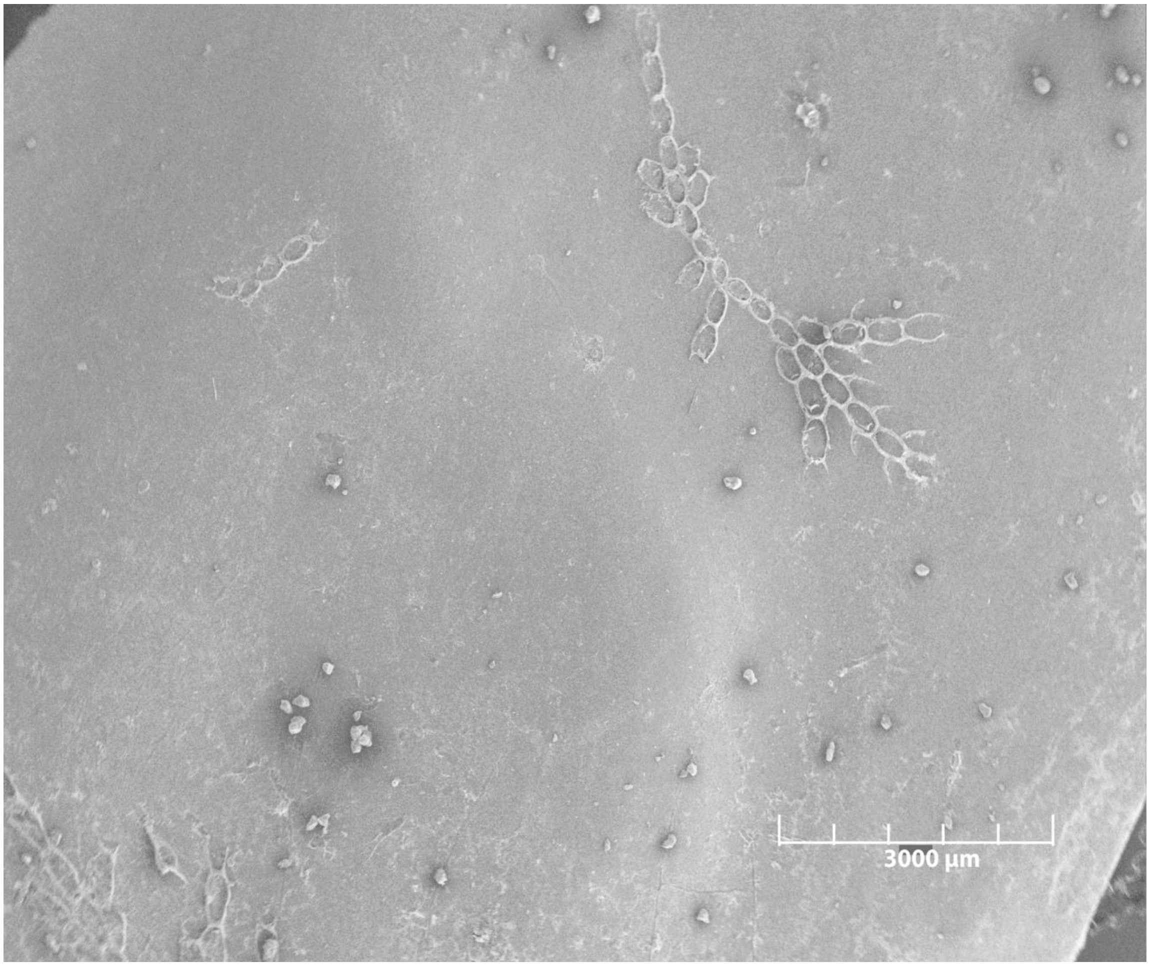

Figure A20, Crassostrea 7, 4 months

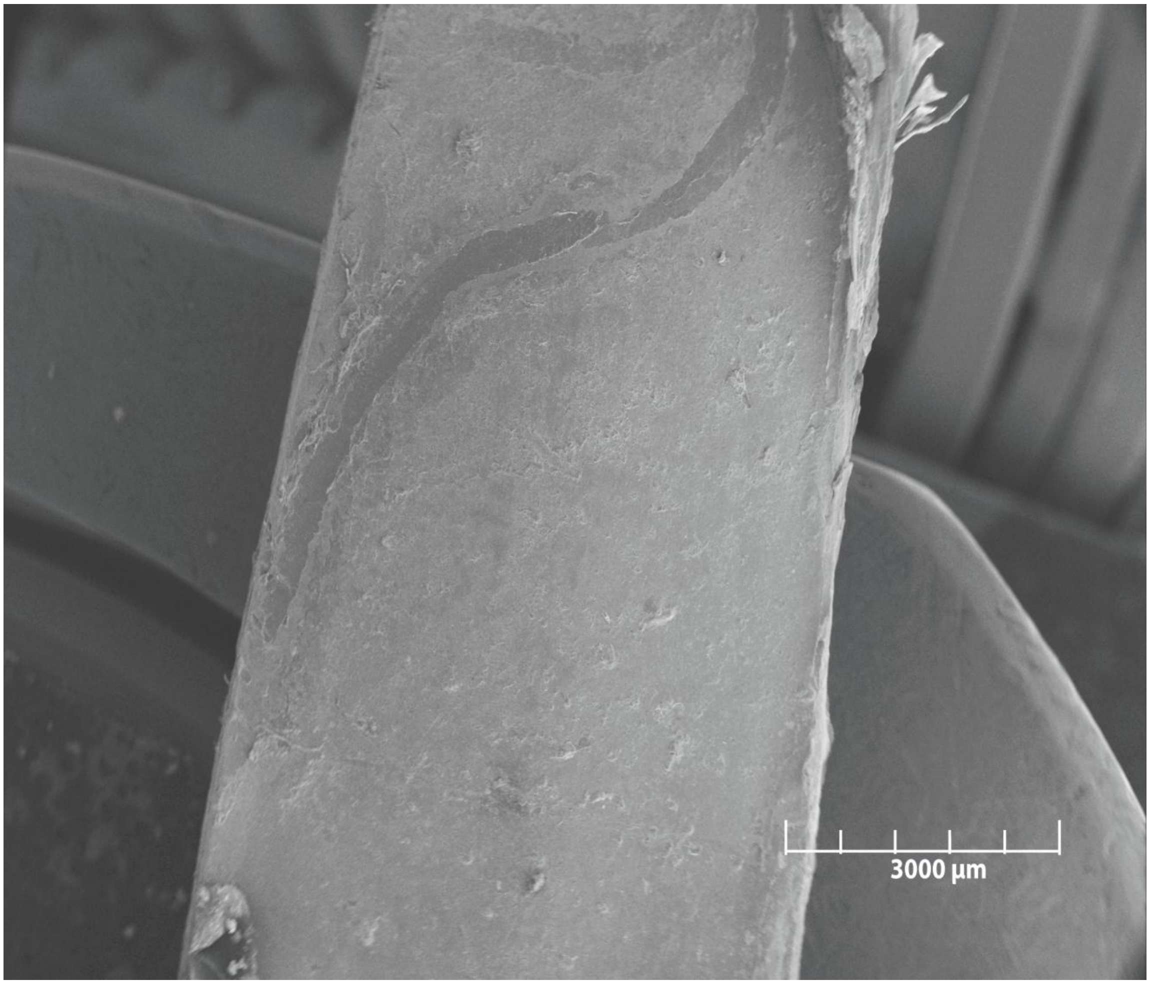

Figure A21, Crassostrea 7, 4 weeks

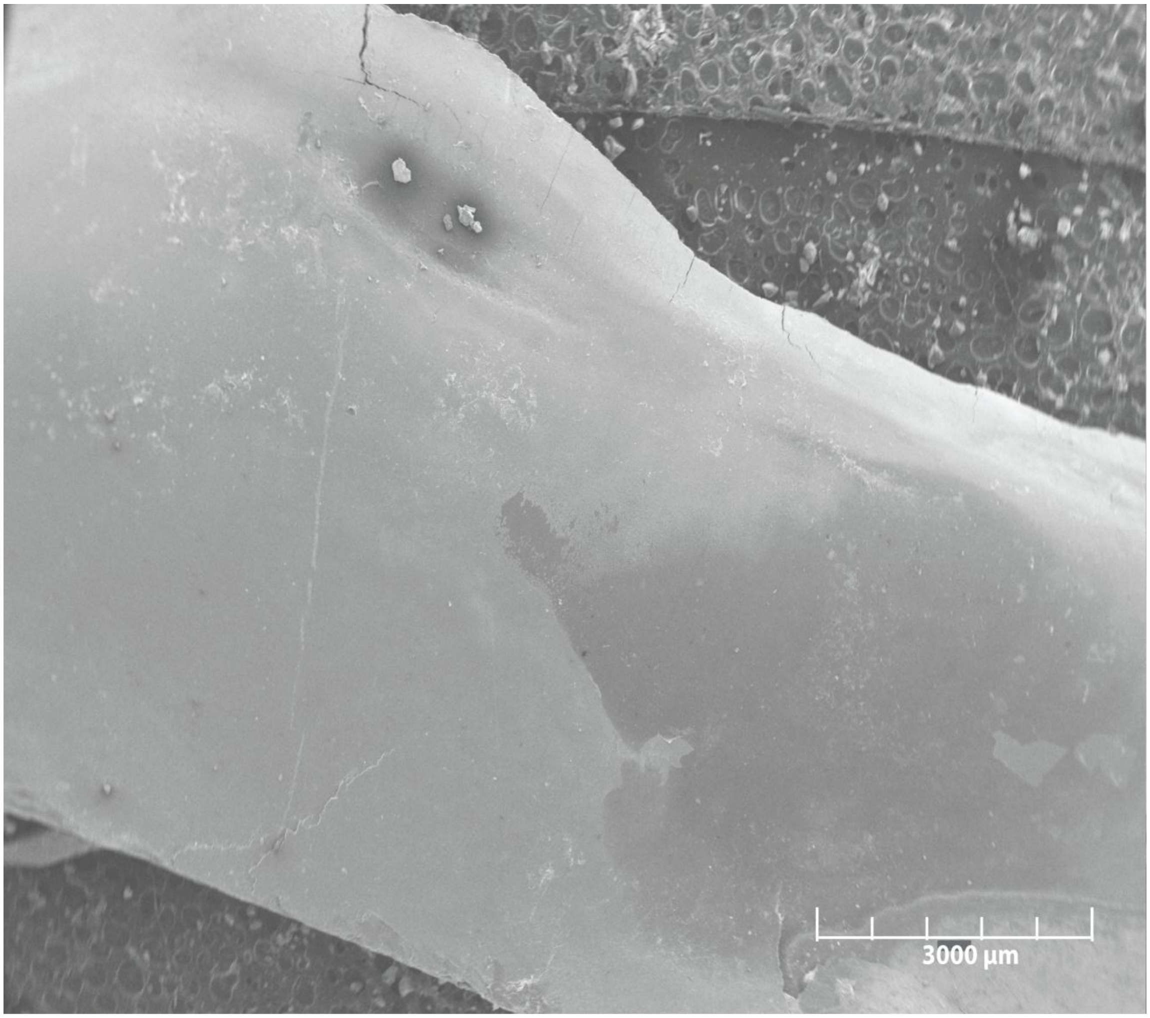

Figure A22, Crassostrea 8, 2 weeks

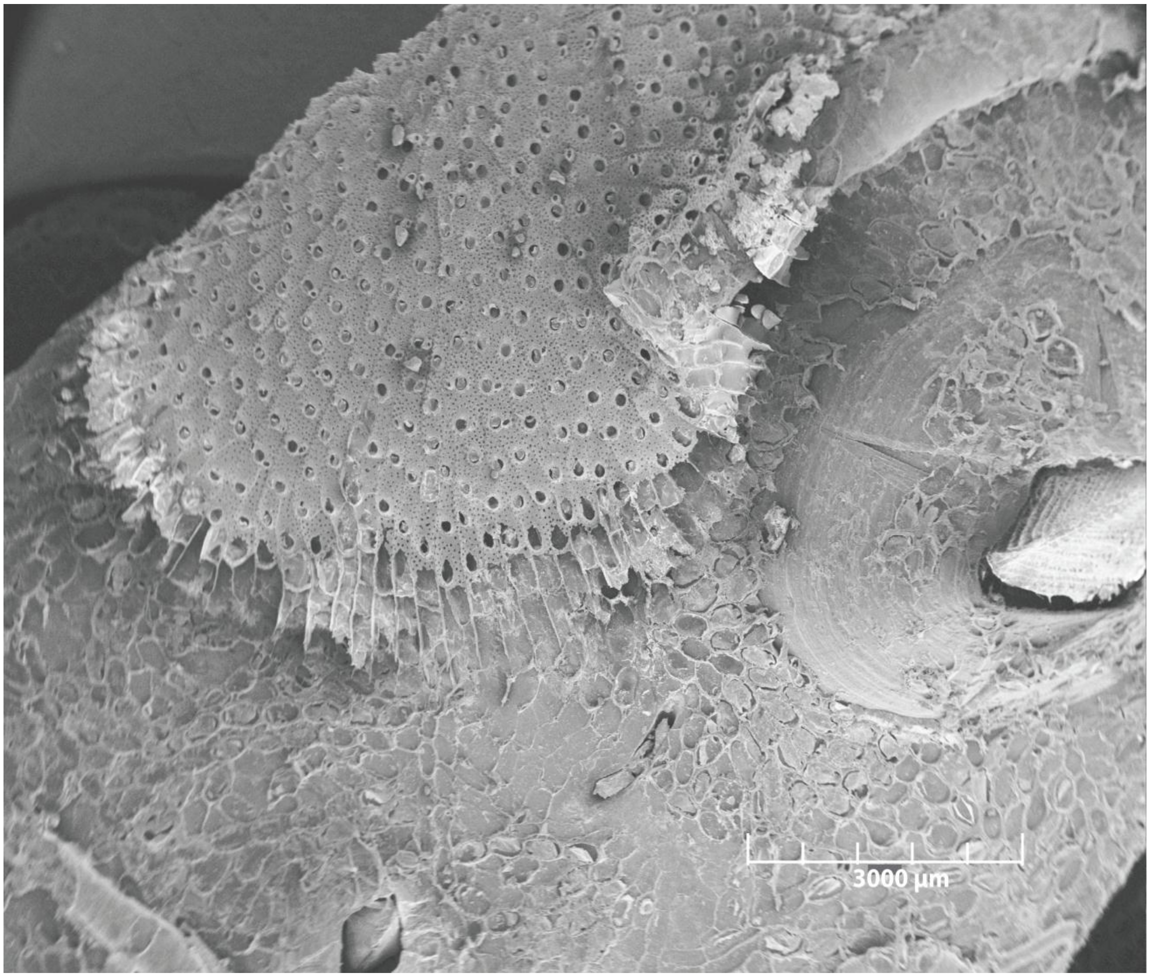

Figure A23, Crassostrea 8, 8 weeks

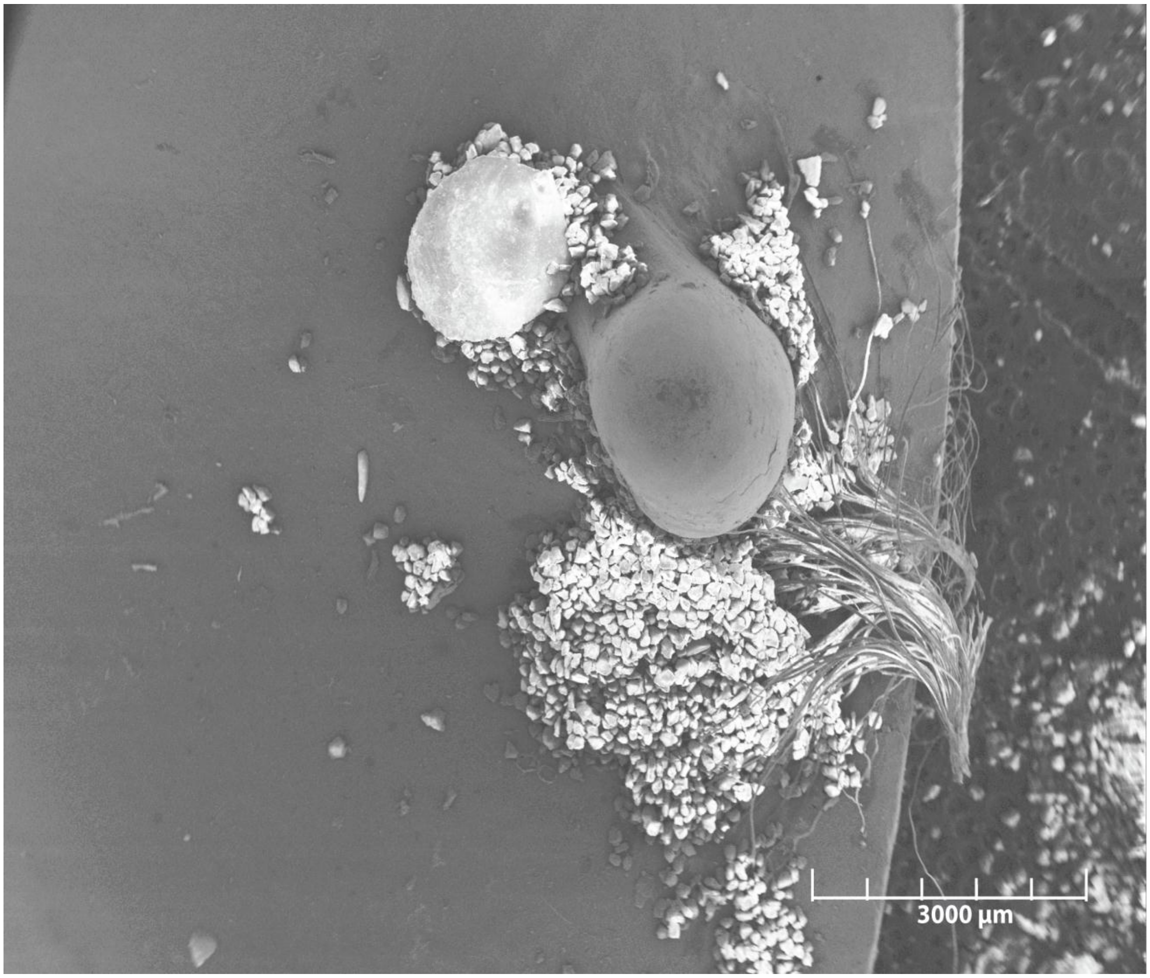

Figure A24, Crassostrea 9, 8 months

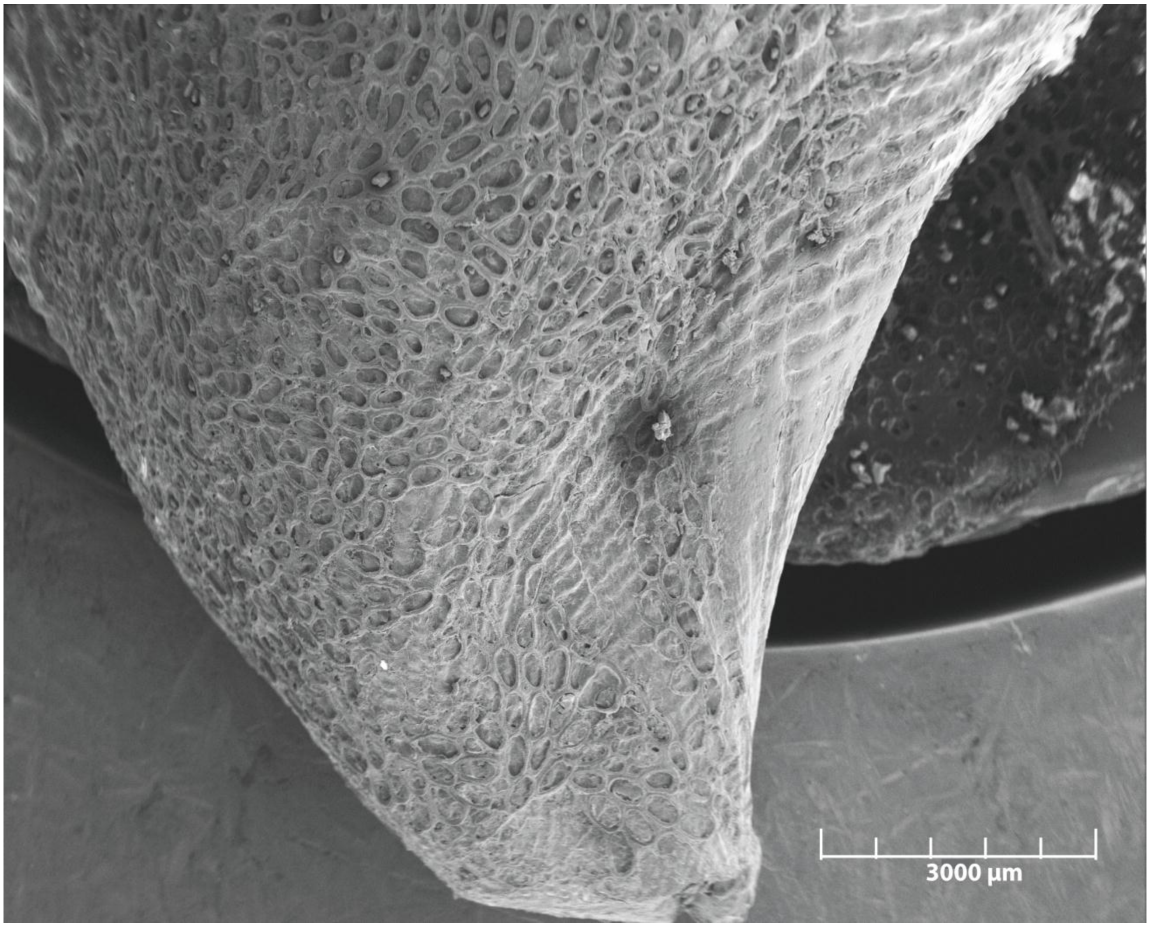

Figure A25, Ischadium 3, 1 year

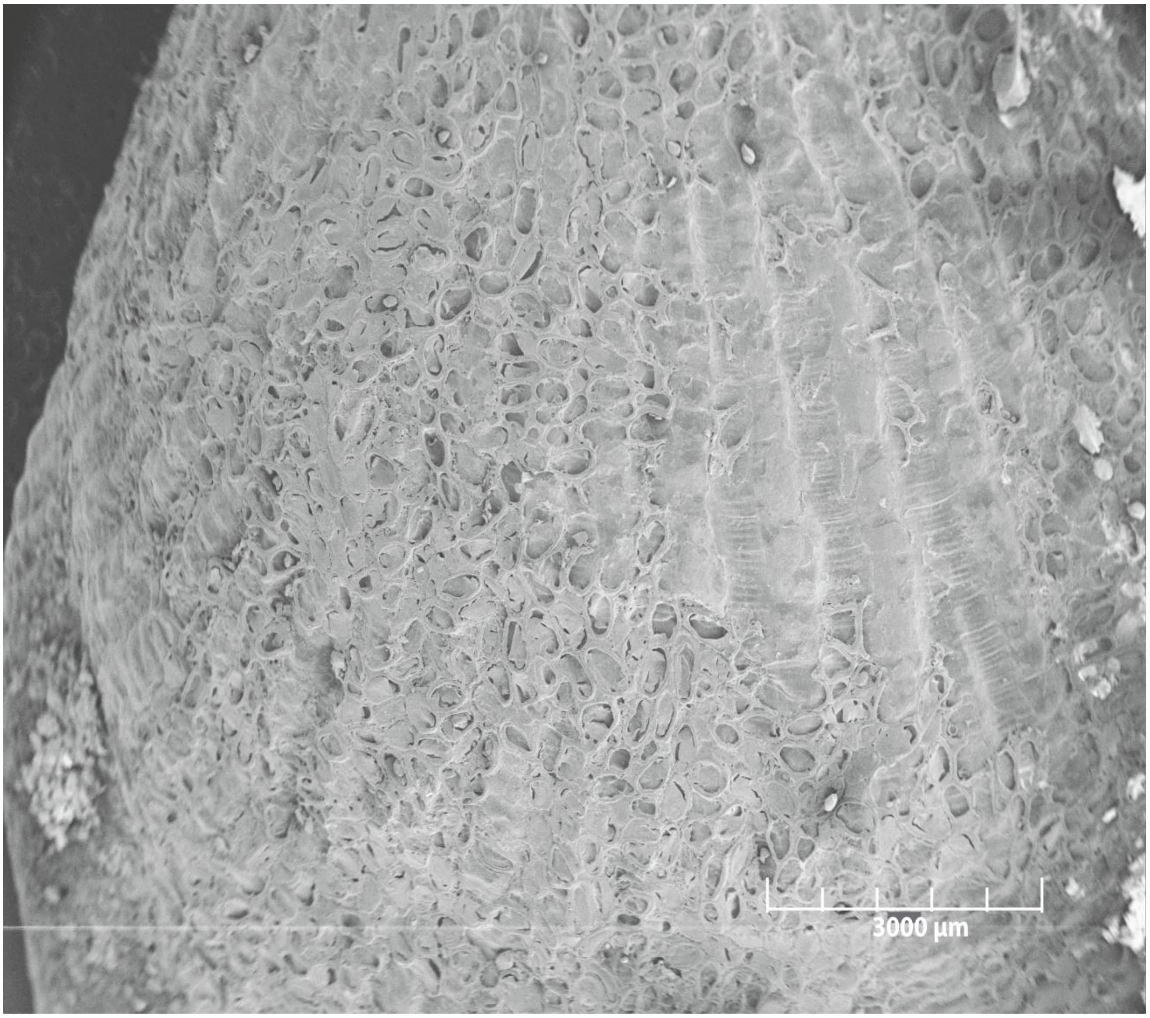

Figure A26, Ischadium 5, 2 weeks

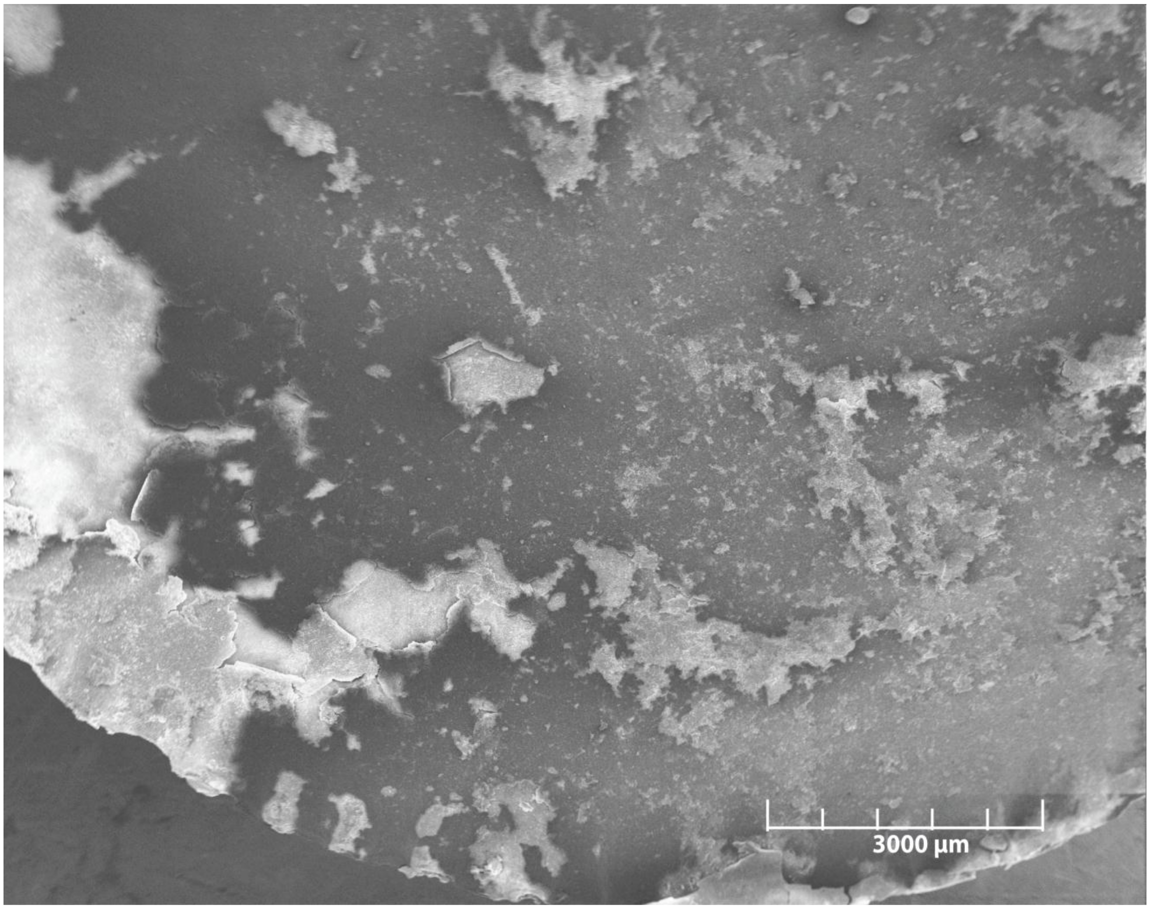

Figure A27, Ischadium 6, 8 weeks

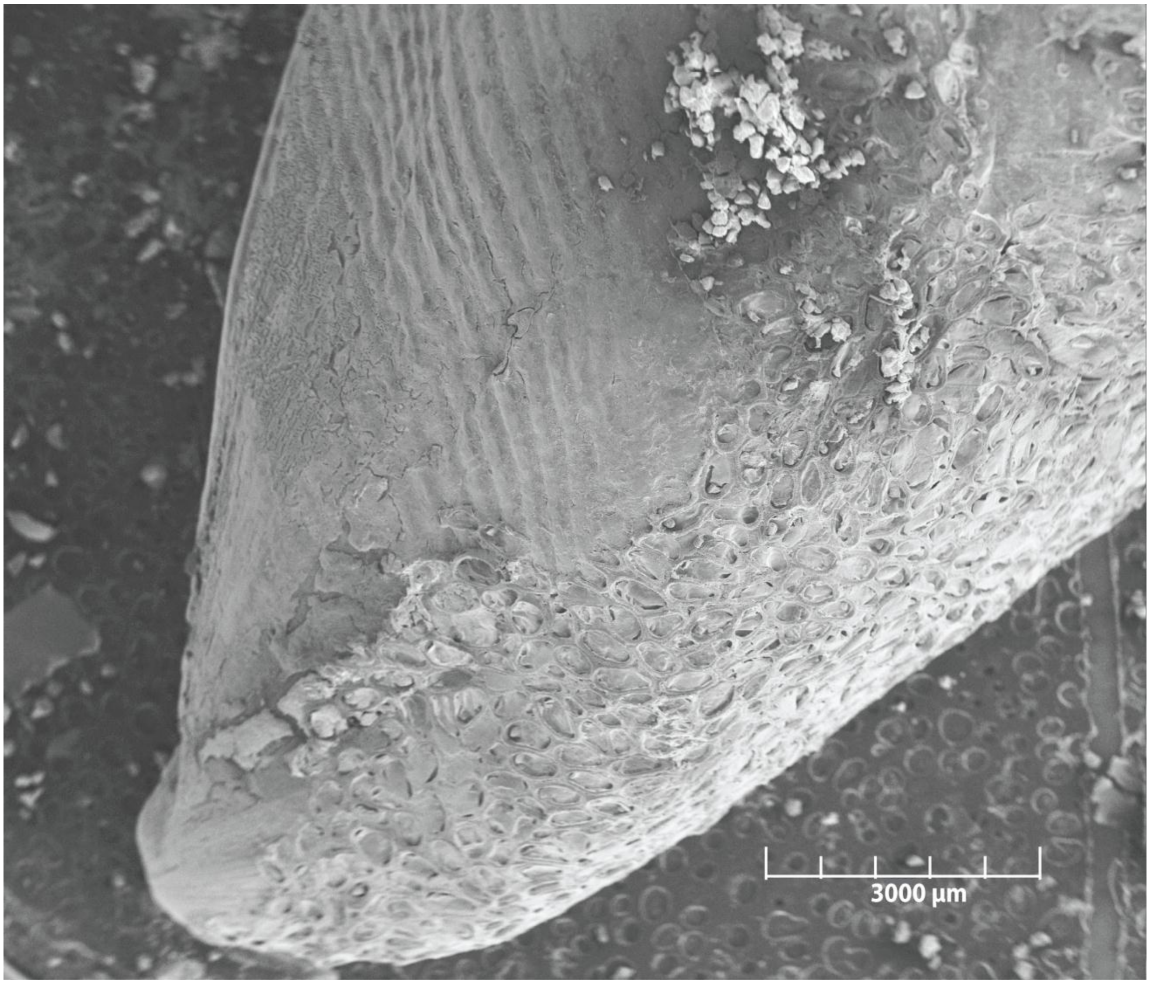

Figure A28, Ischadium 8, 4 weeks

Figure A29, Ischadium 9, 1 year

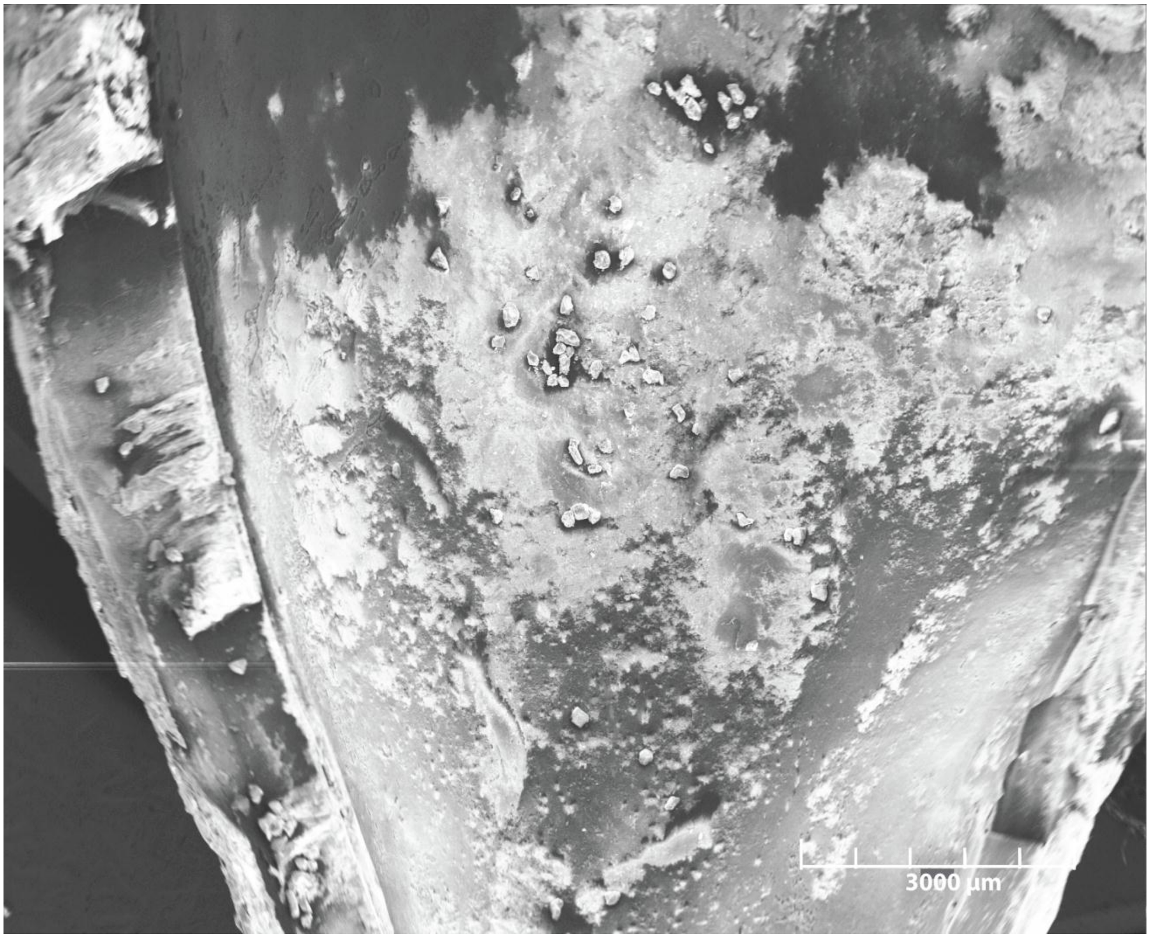

Figure A30, Ischadium 10, 4 weeks

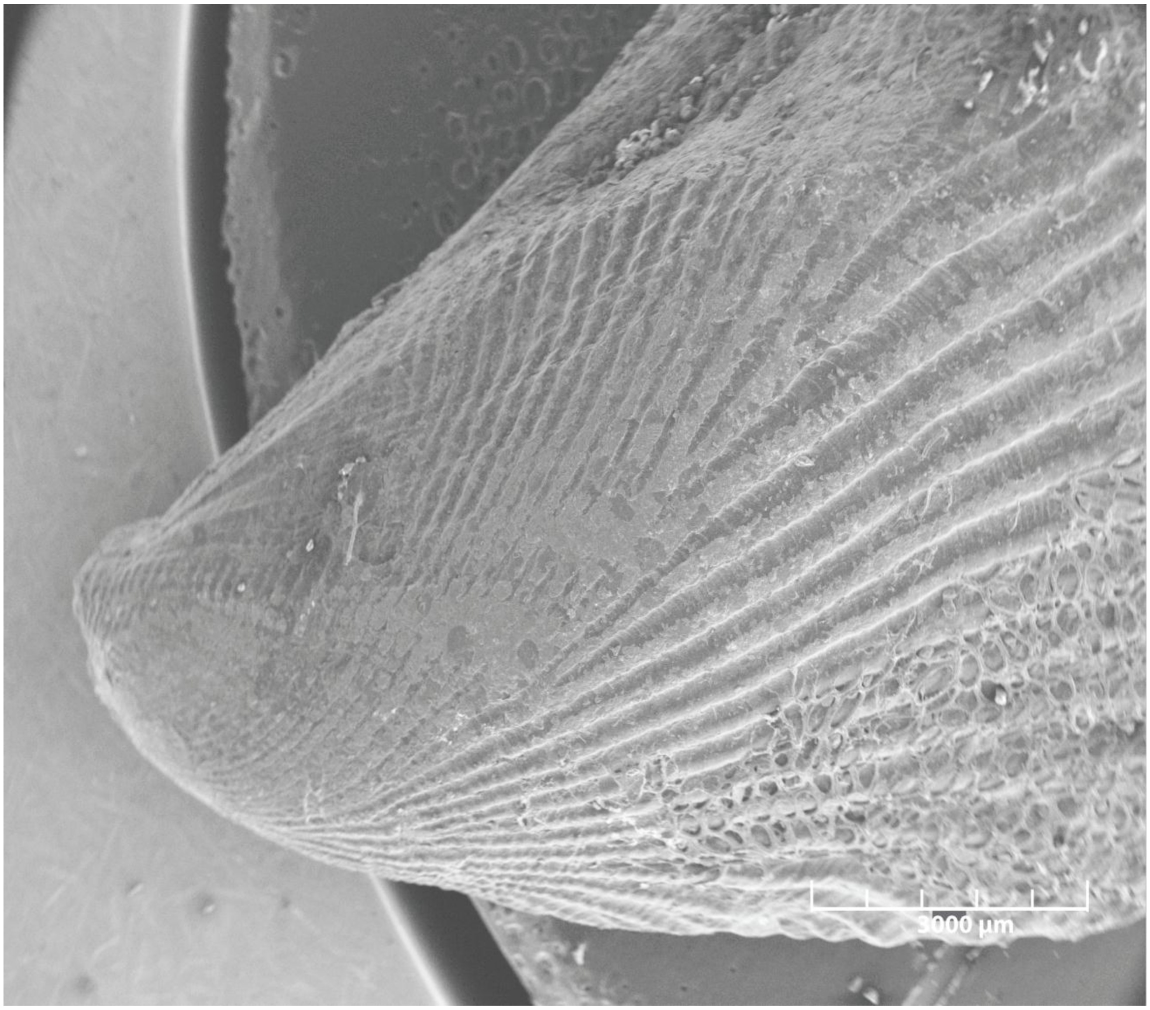

Figure A31, Ischadium 11, 8 months

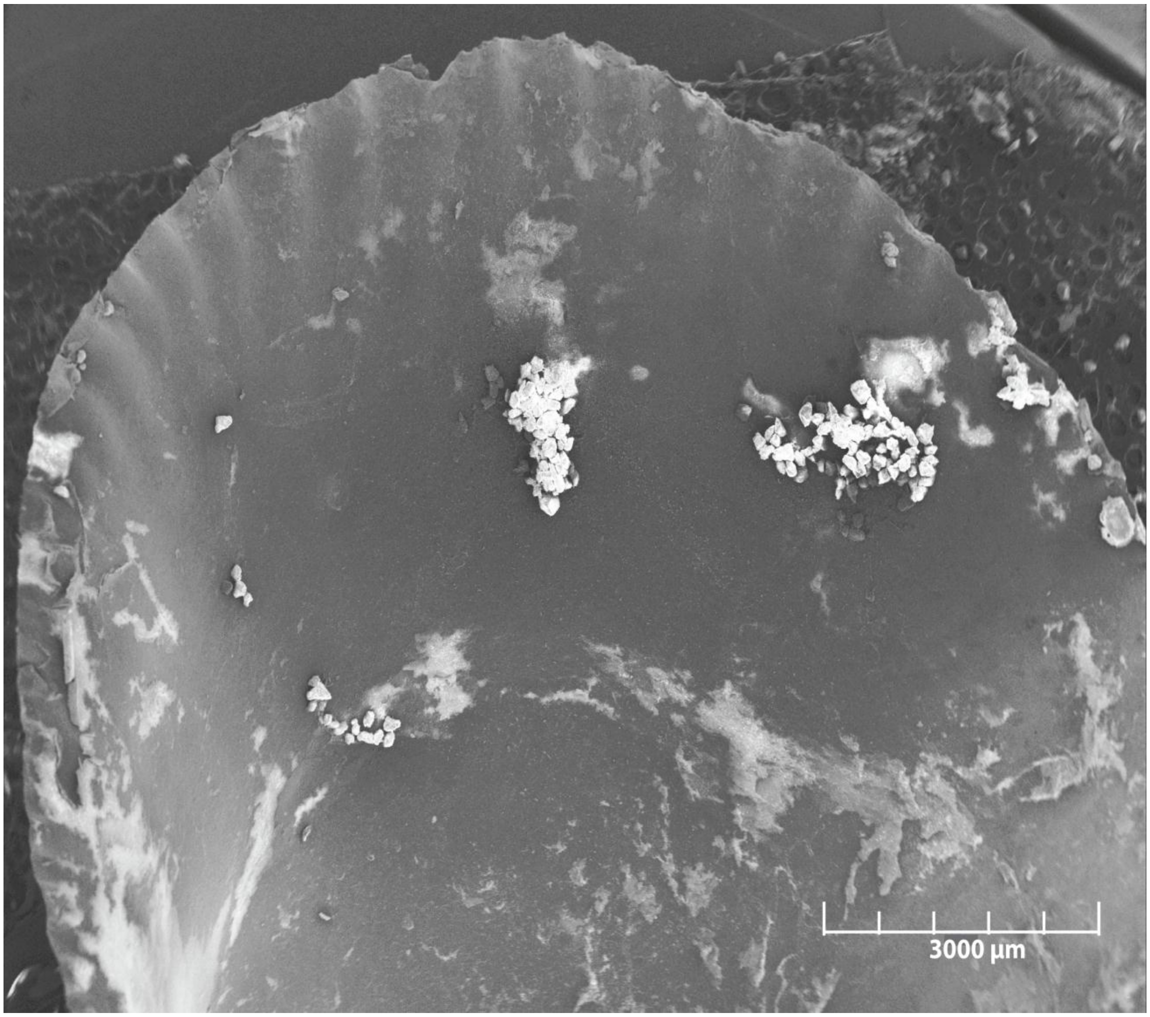

Figure A32, Ischadium 12, 1 year

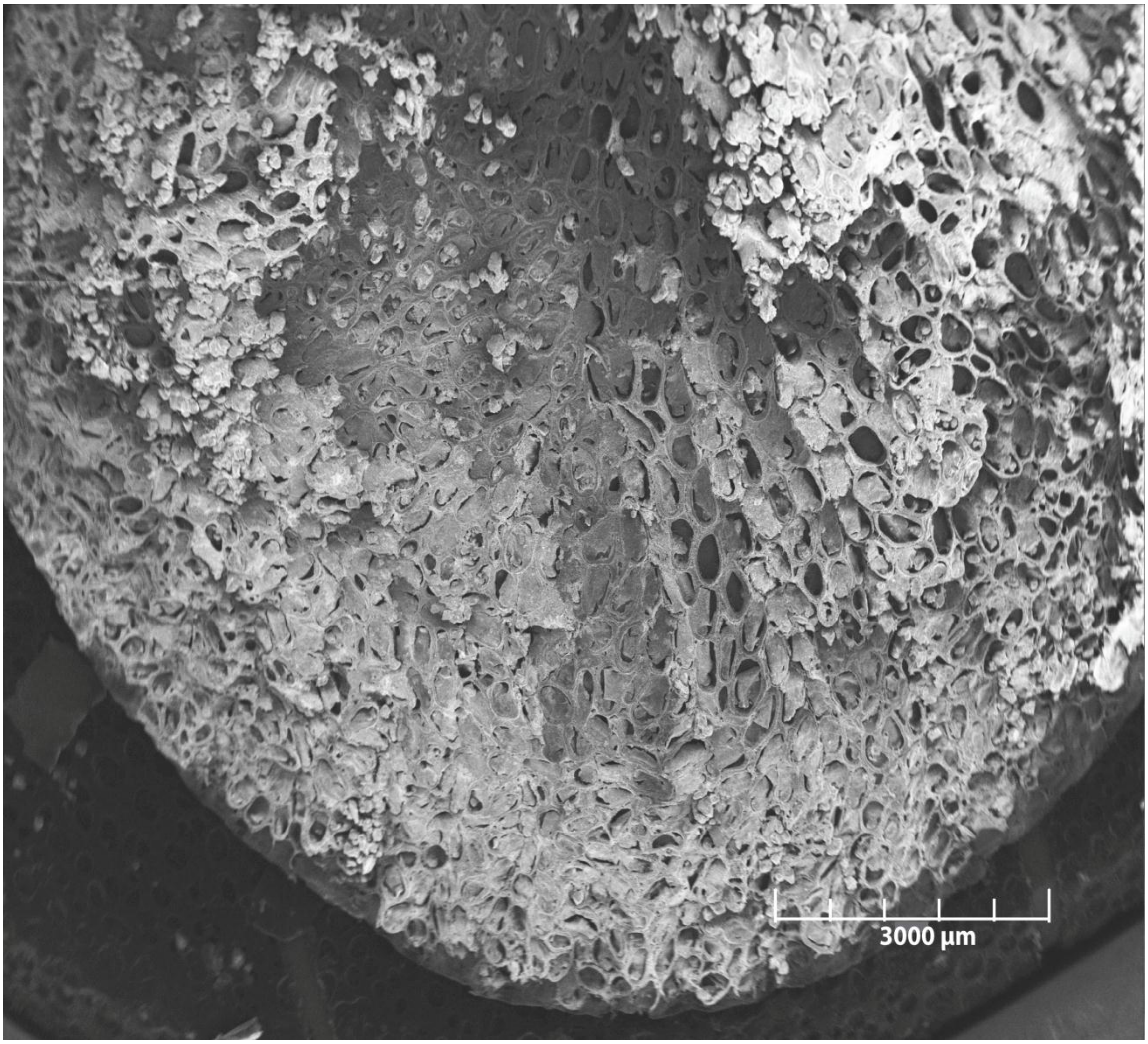

Figure A33, Ischadium 13, 2weeks

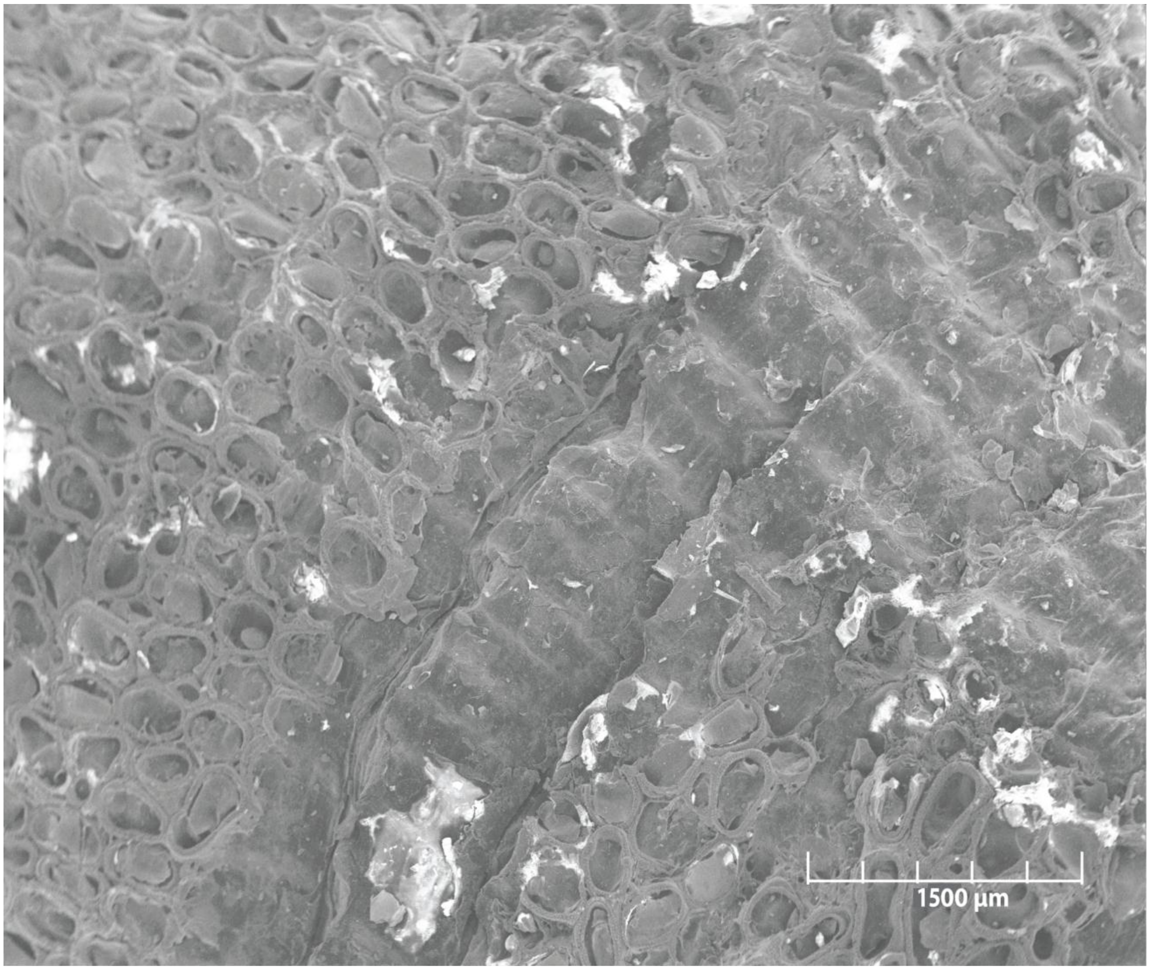

Figure A34, Ischadium 15, 4 months

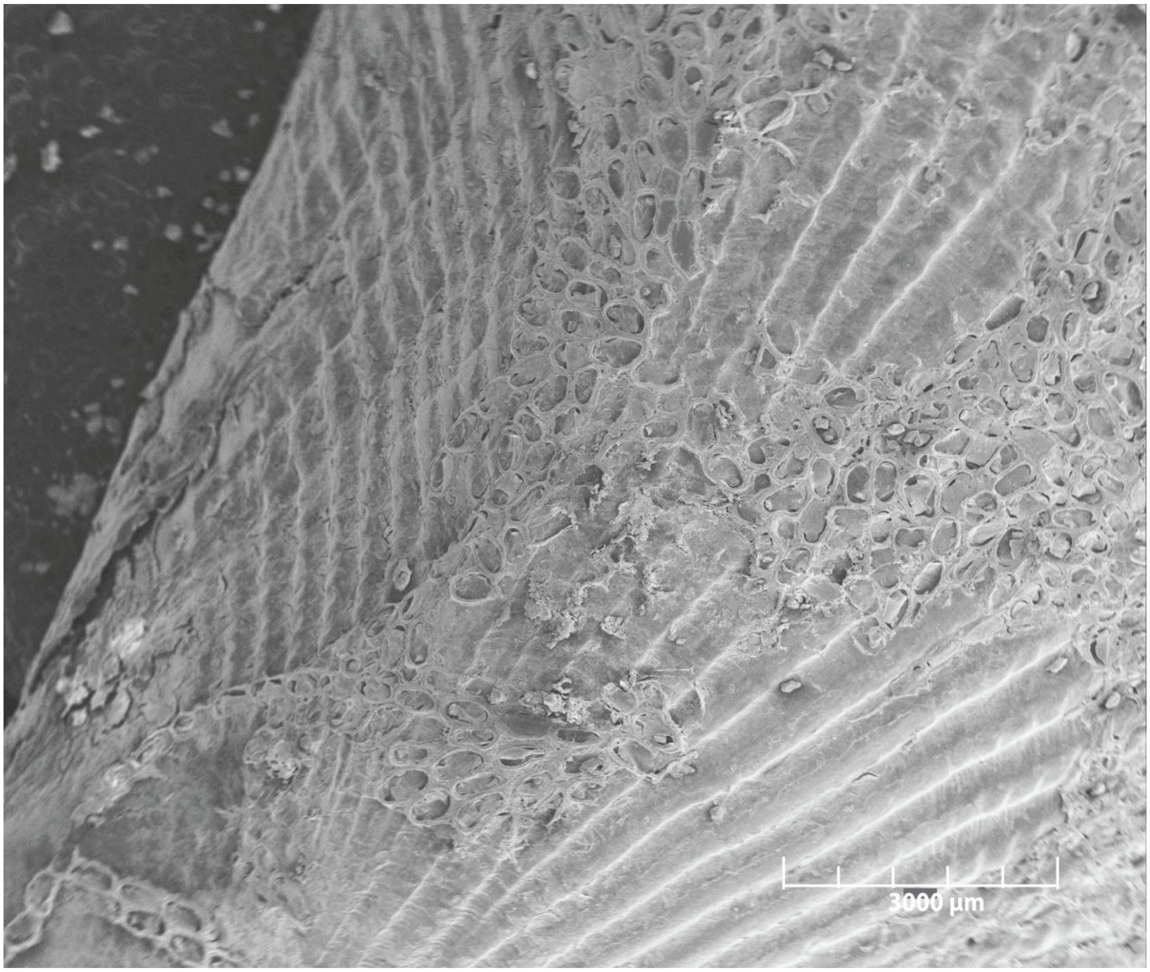

Figure A35, Ischadium 16, 8 weeks

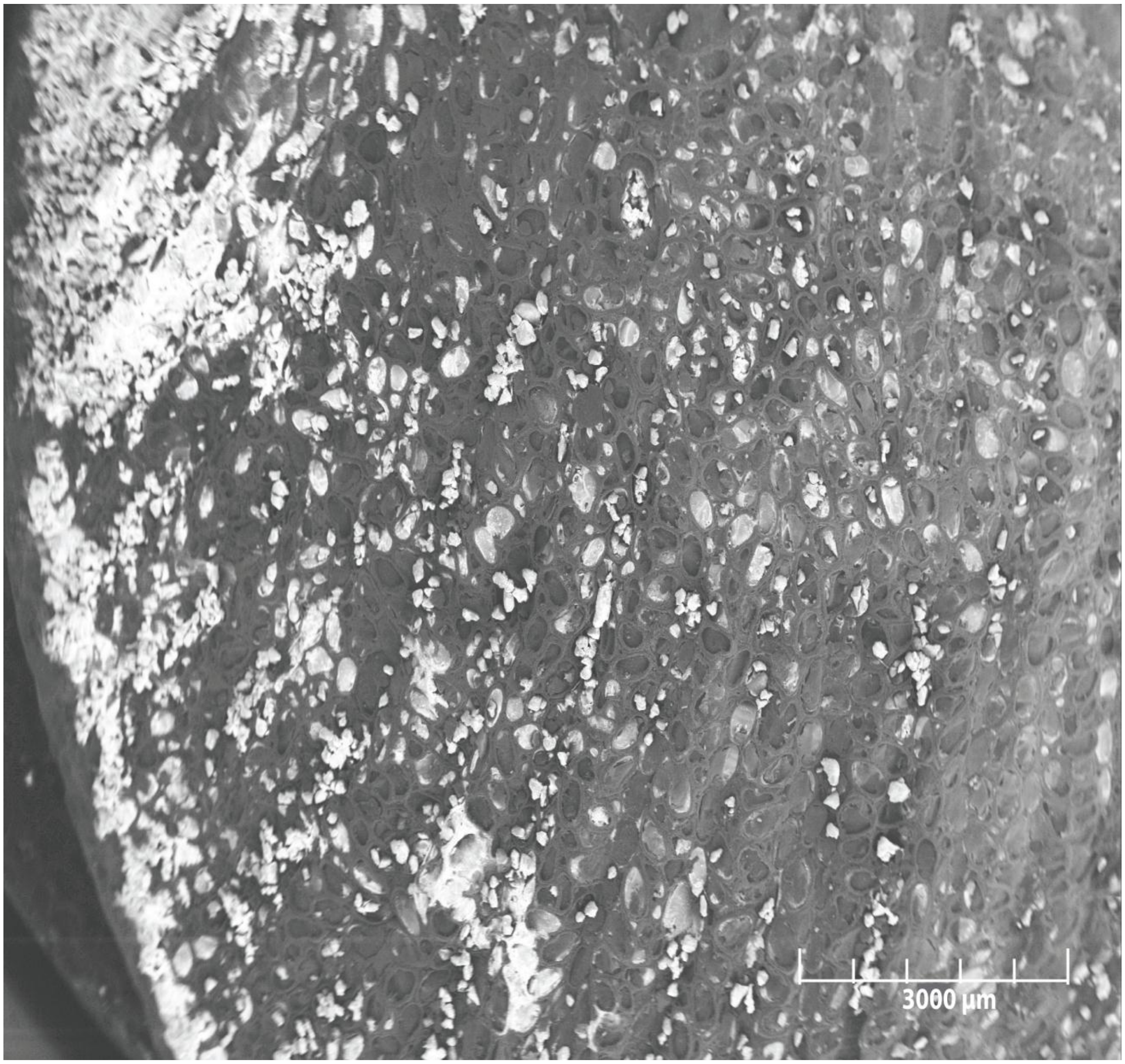

Figure A36, Ischadium 18, 8 months

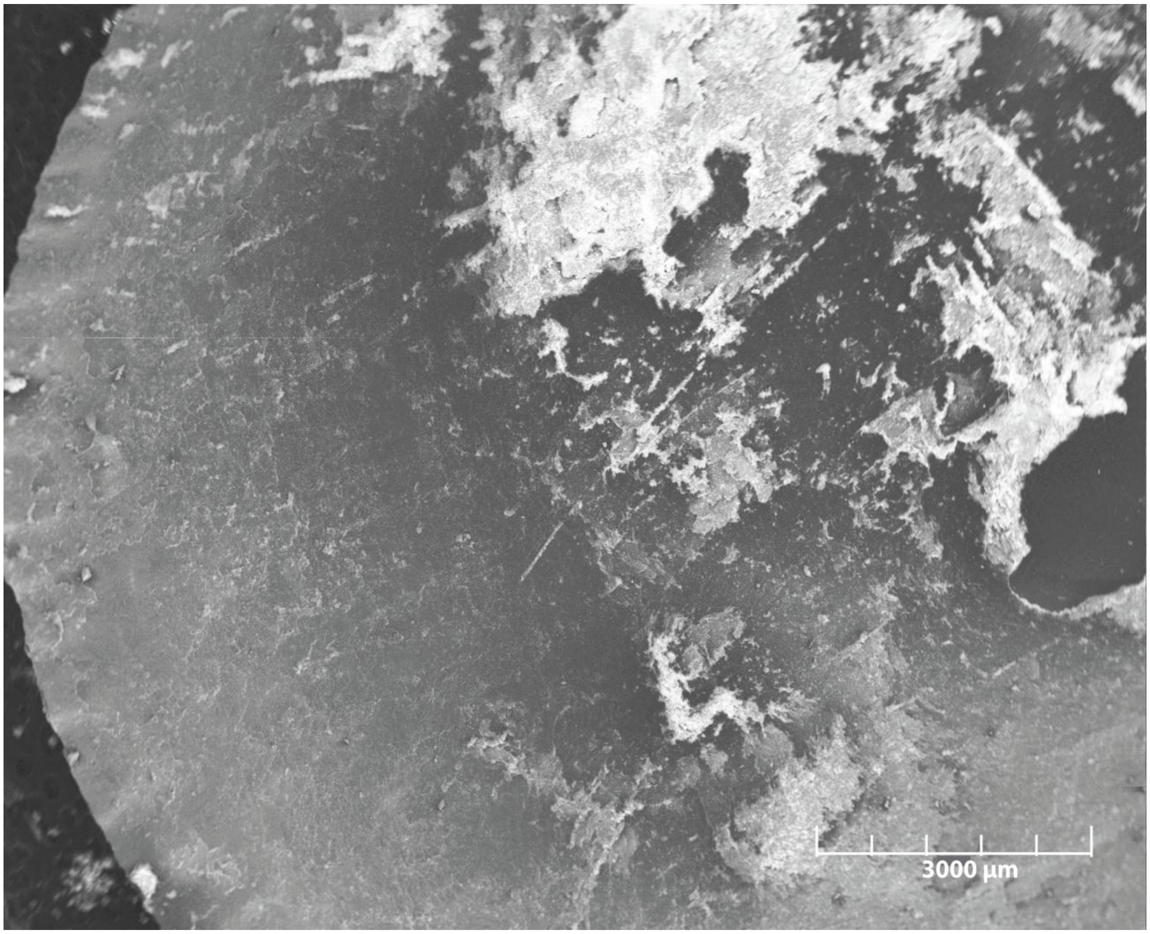

Figure A37, Ischadium 19, 8 months

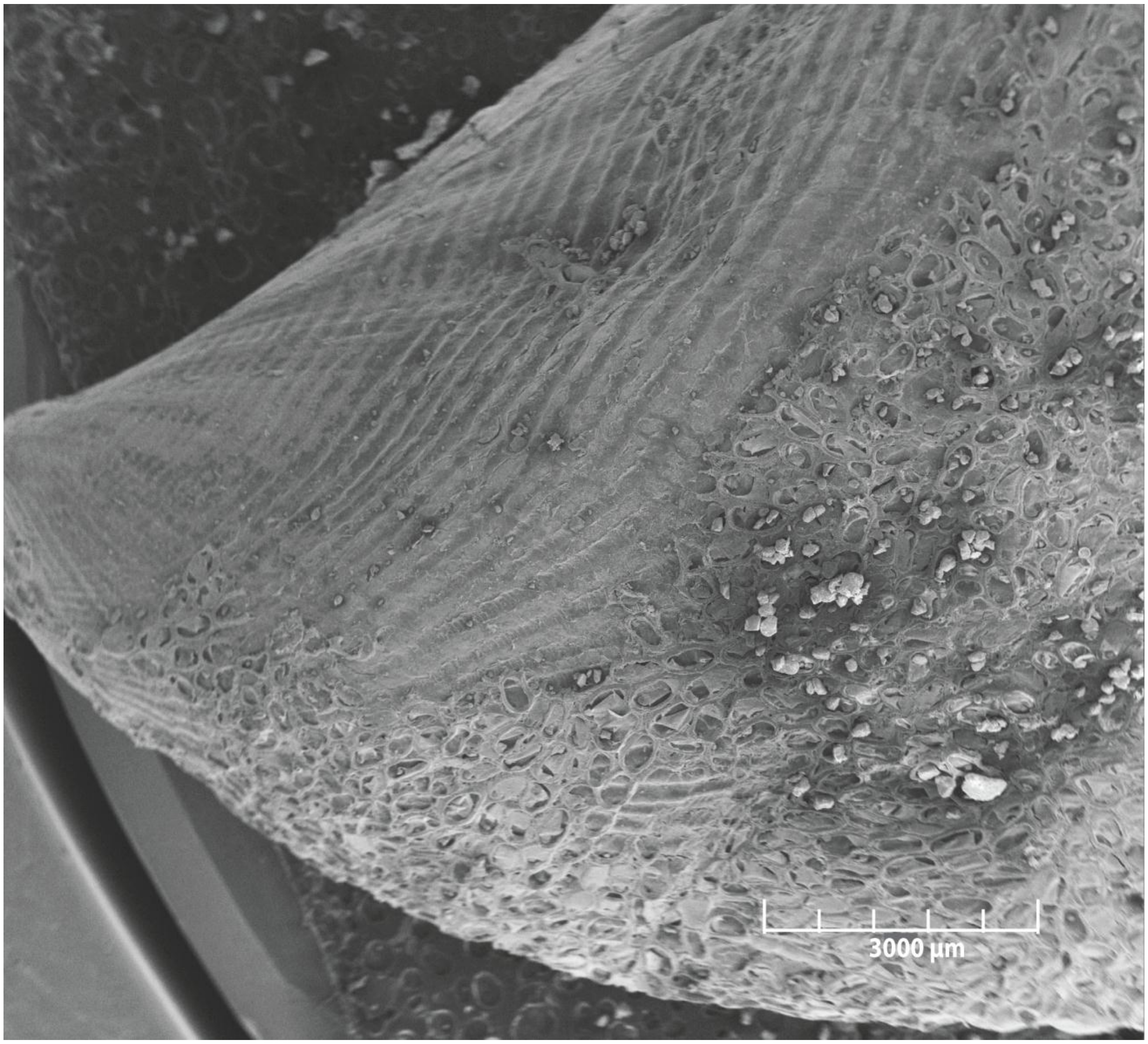

Figure A38, Ischadium 20, 4 months

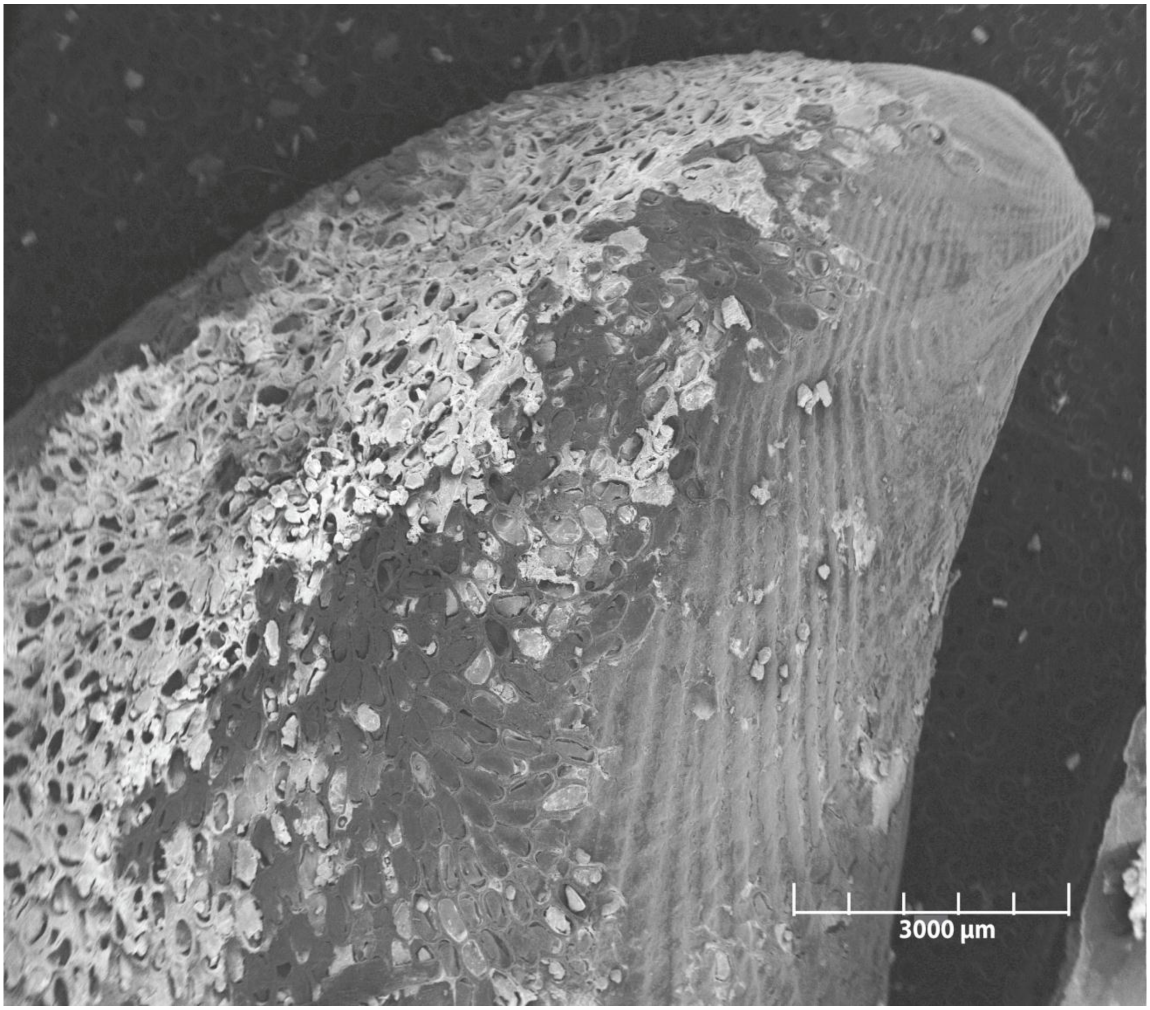

Figure A39, Ischadium 21, 4 weeks

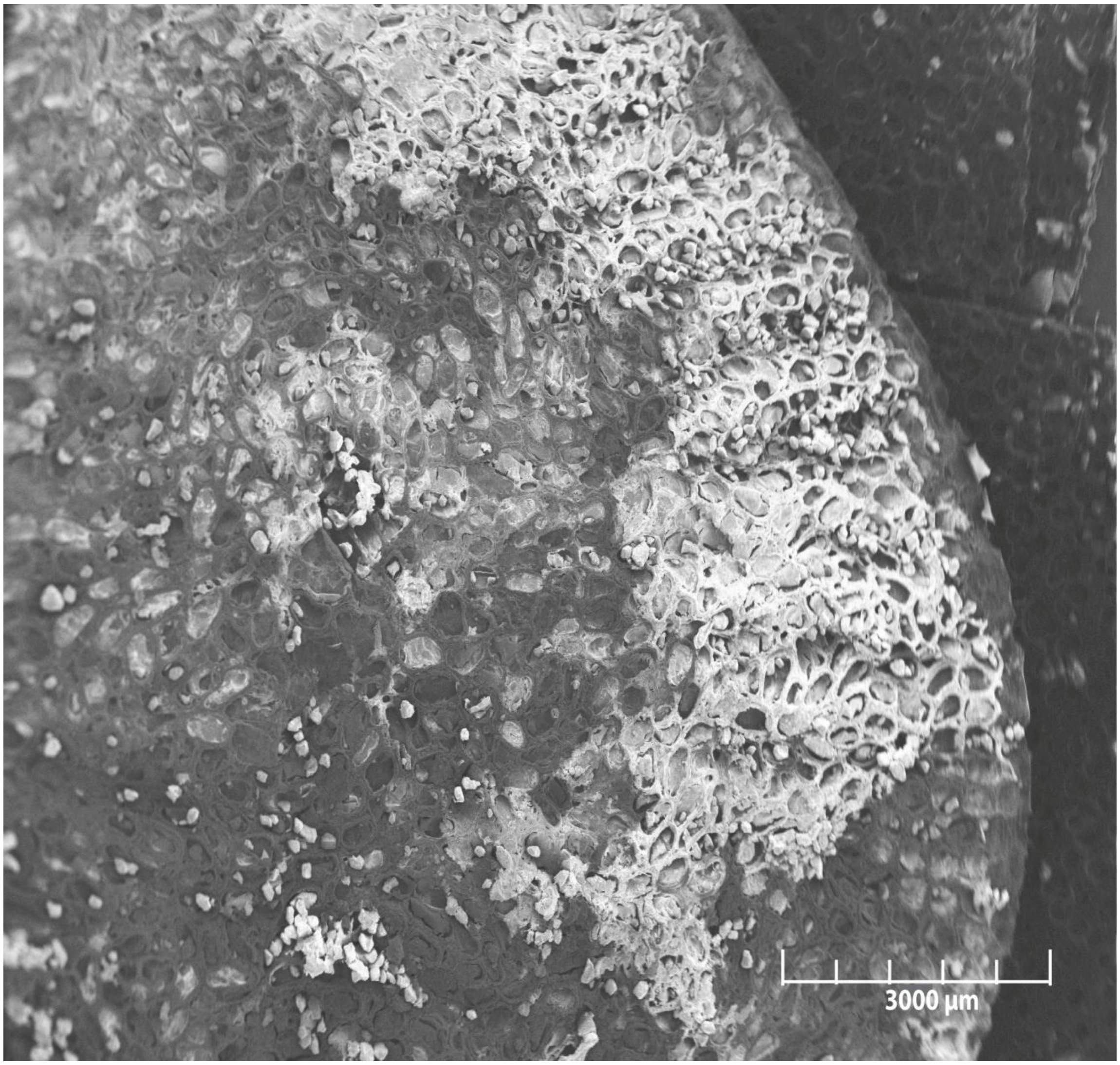

Figure A40, Ischadium 23, 4 months

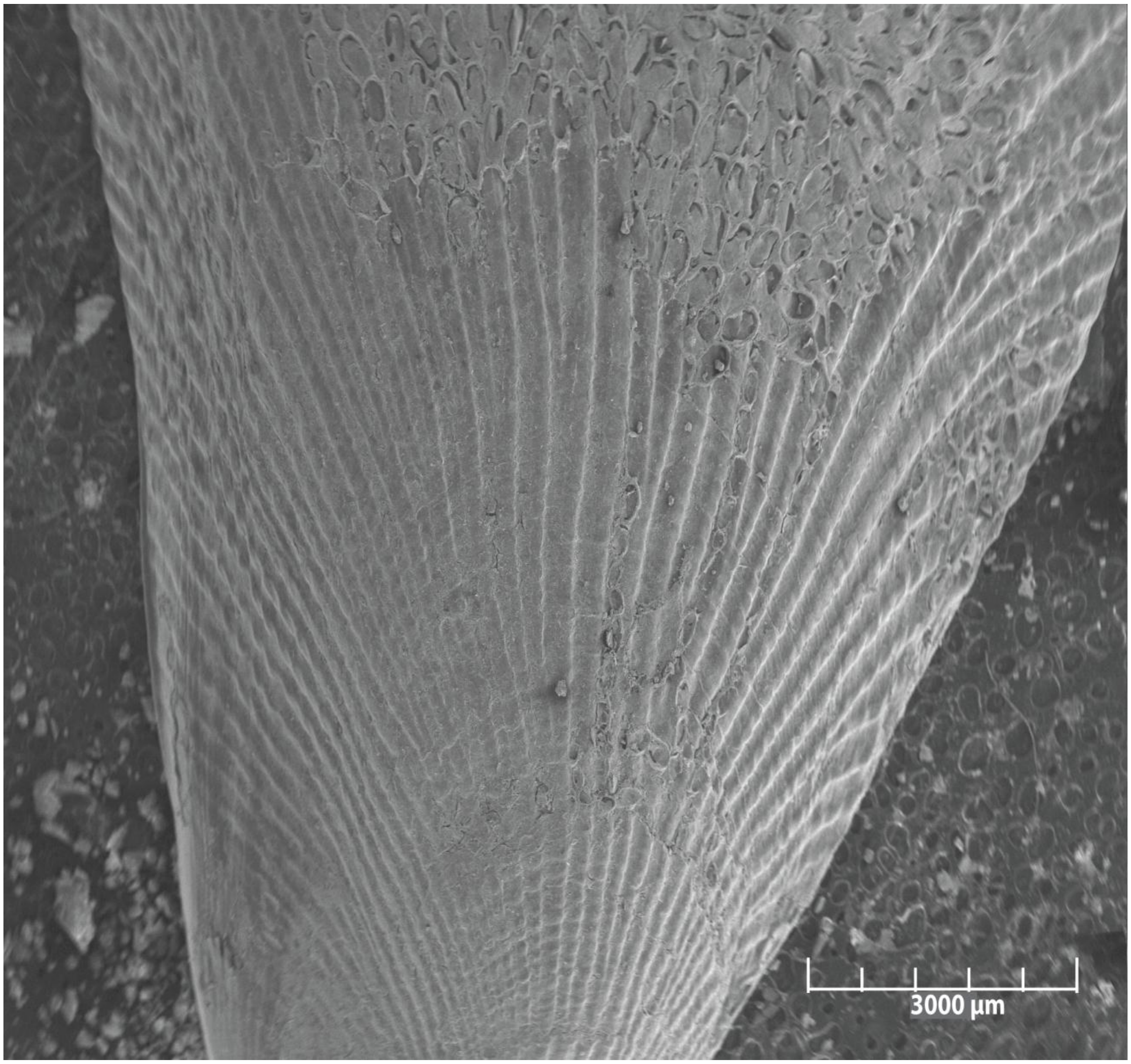

Figure A41, Ischadium 26, 2 weeks

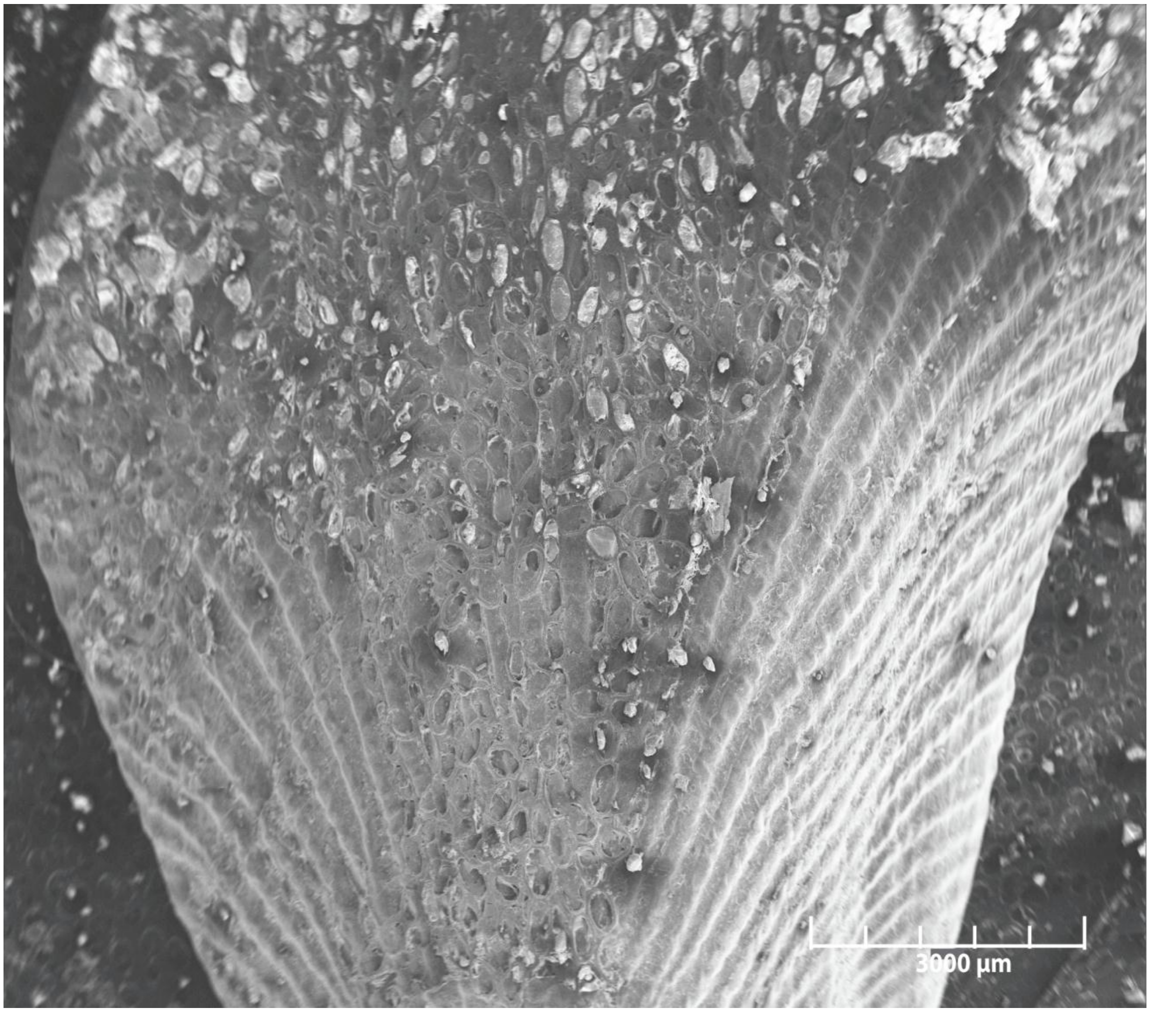

Figure A42, Ischadium 27, 8 weeks

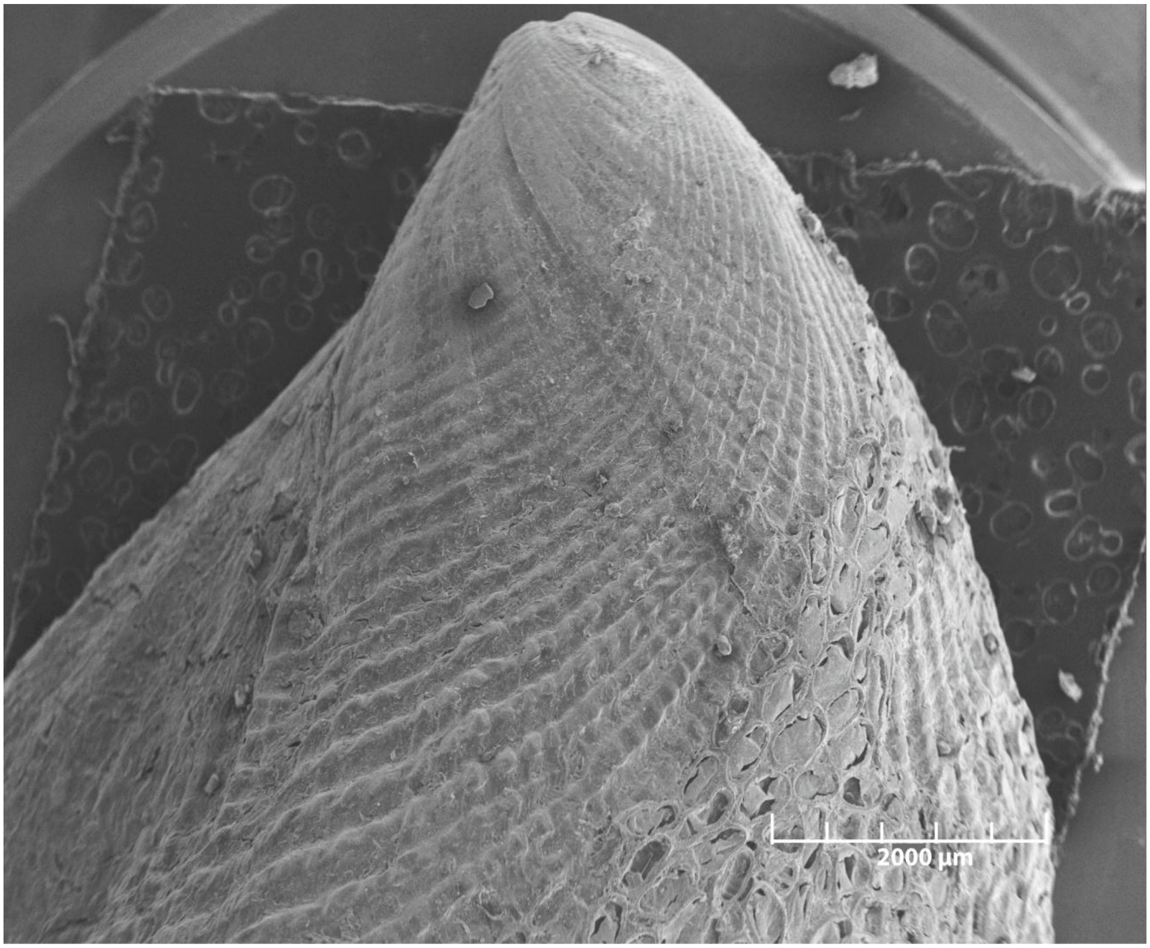

Figure A43, Ischadium 28, 2 weeks

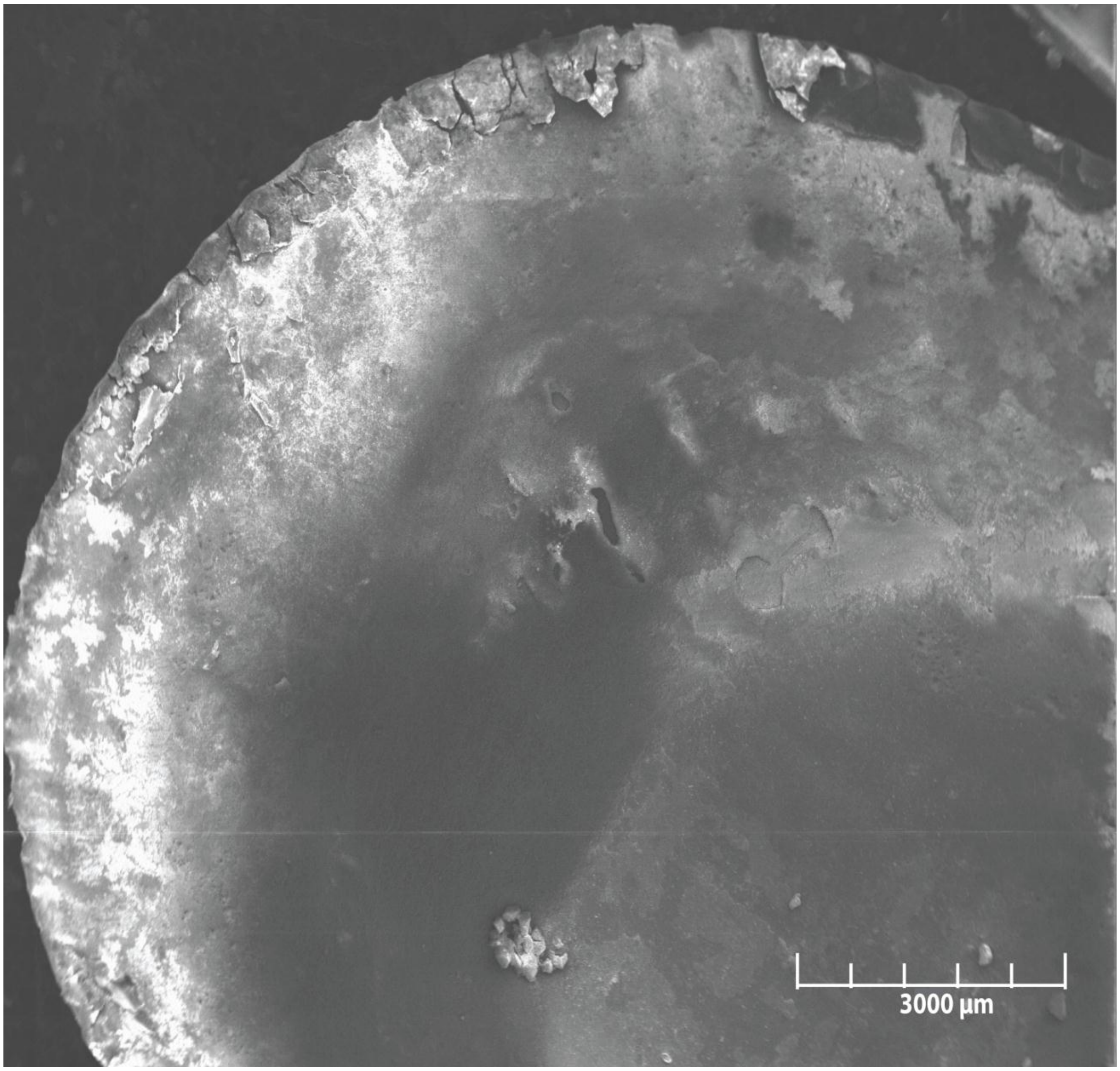

Figure A44, Ischadium 29, 1 year

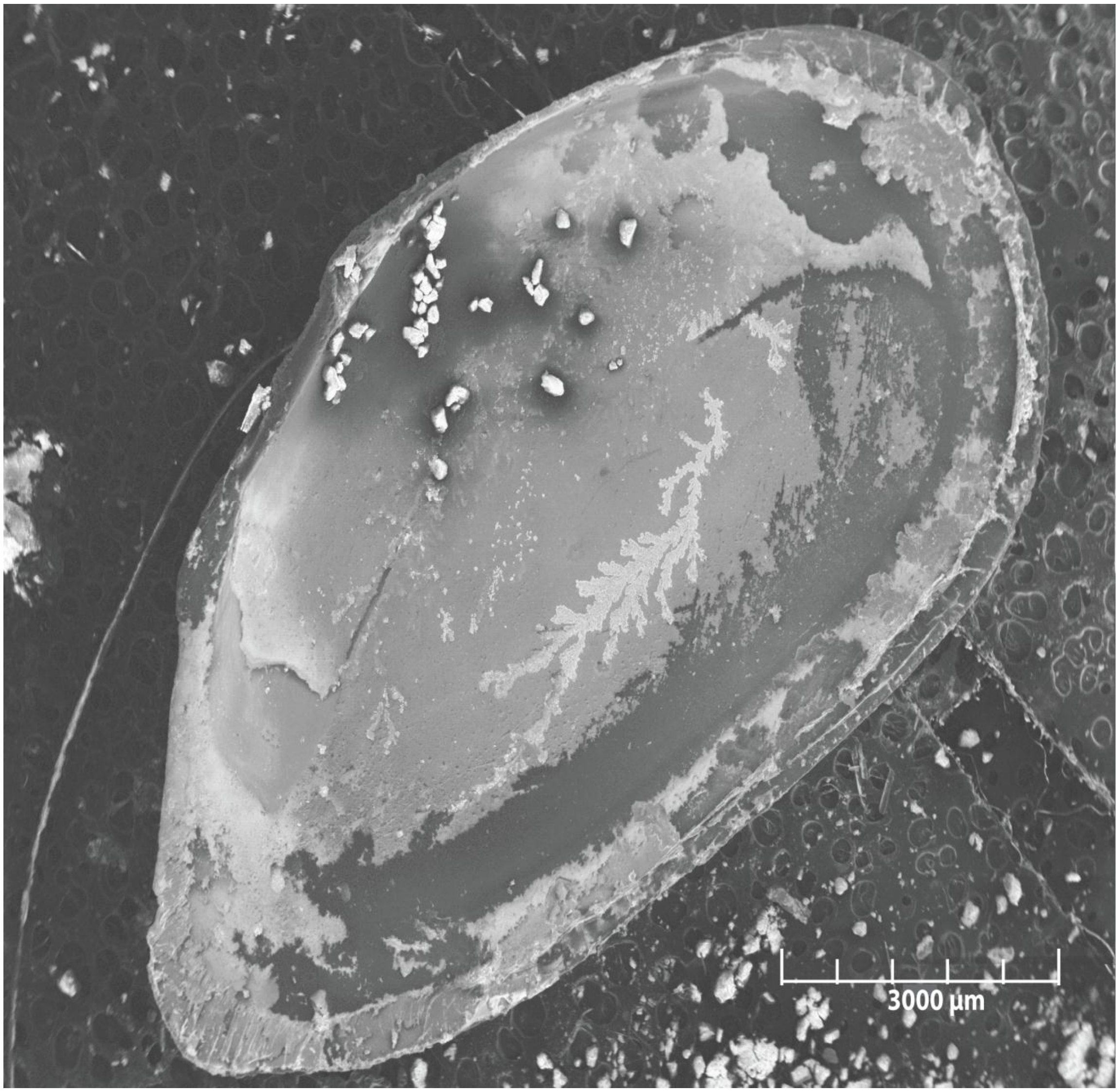

Figure A45, Macoma 2, 8 months

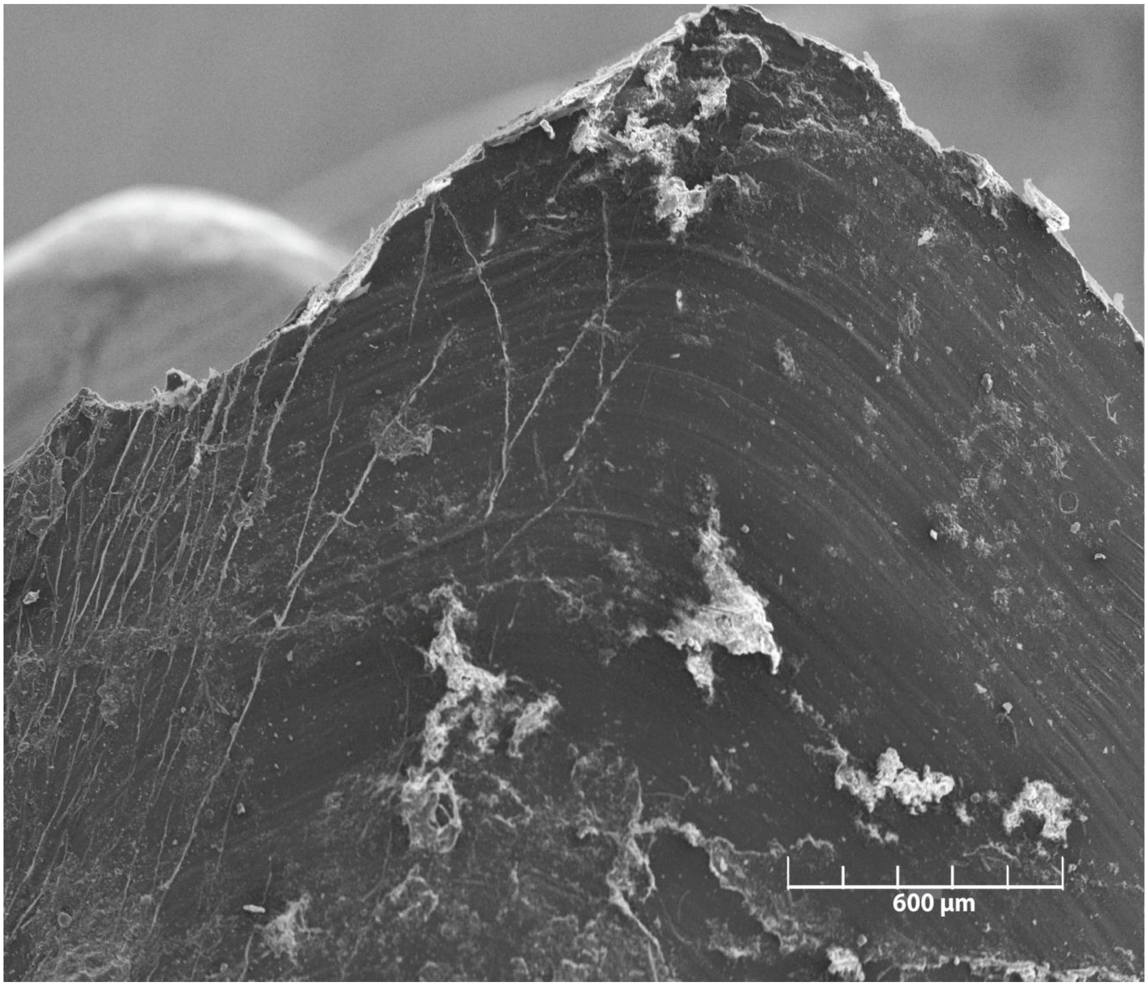

Figure A46, Macoma 3, 8 weeks

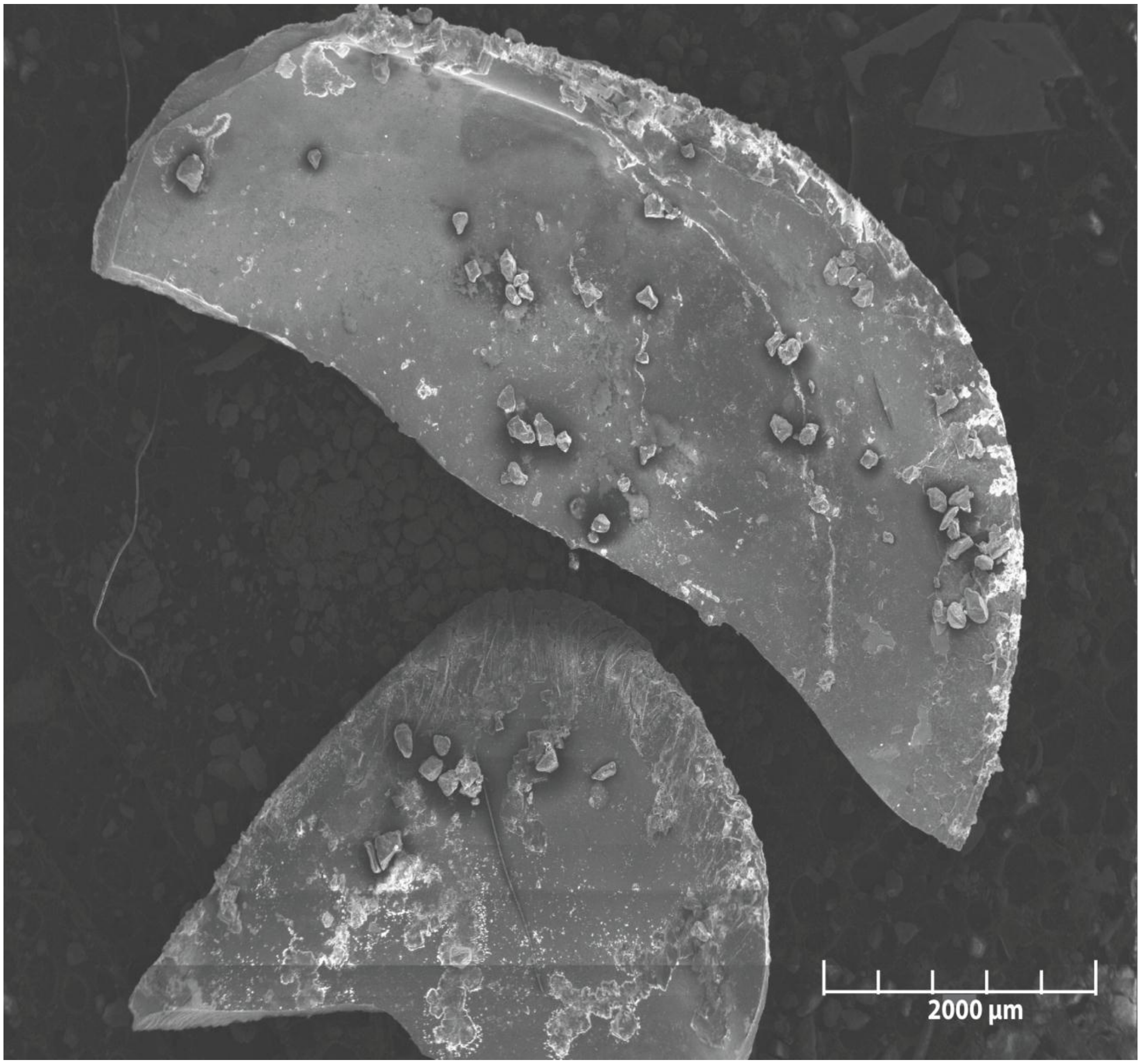

Figure A47, Macoma 6, 1 year

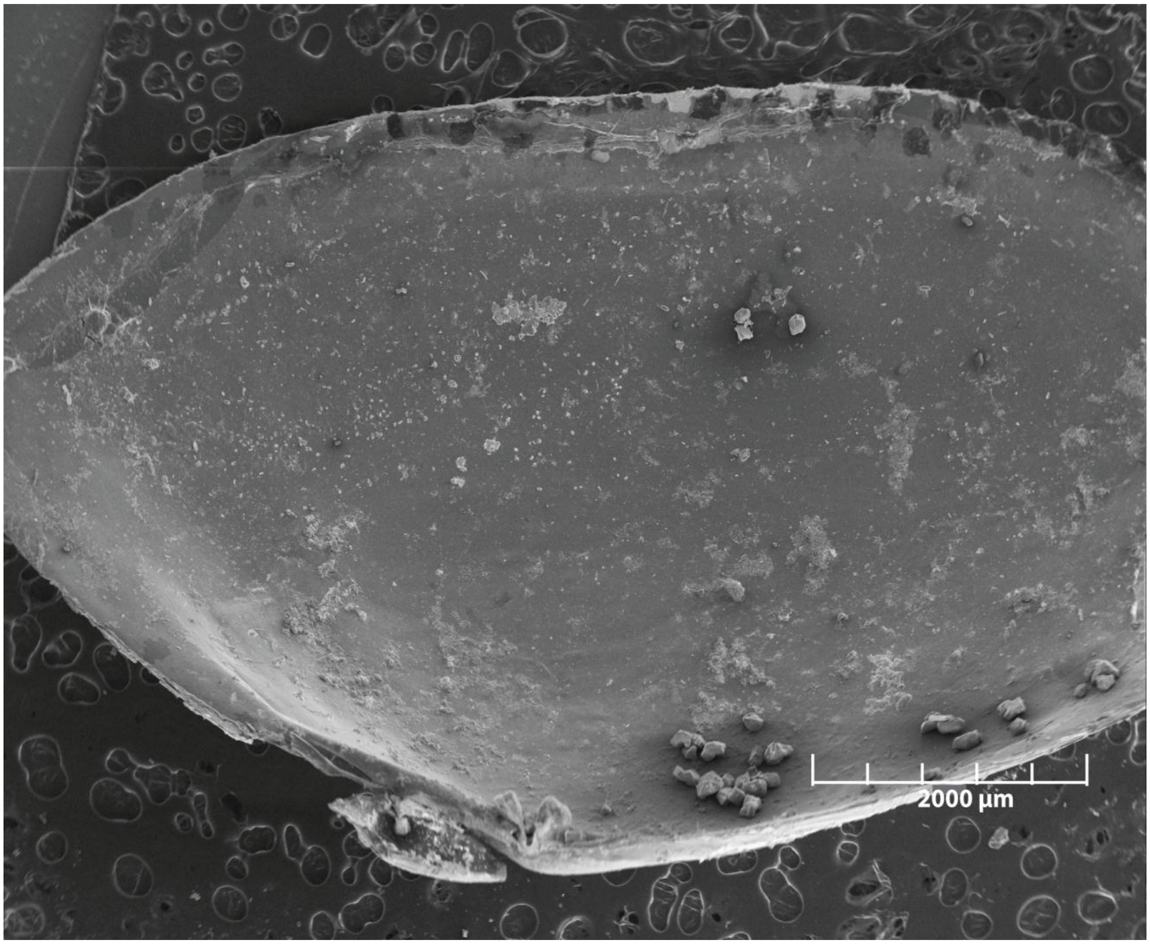

Figure A48, Macoma 8, 4weeks

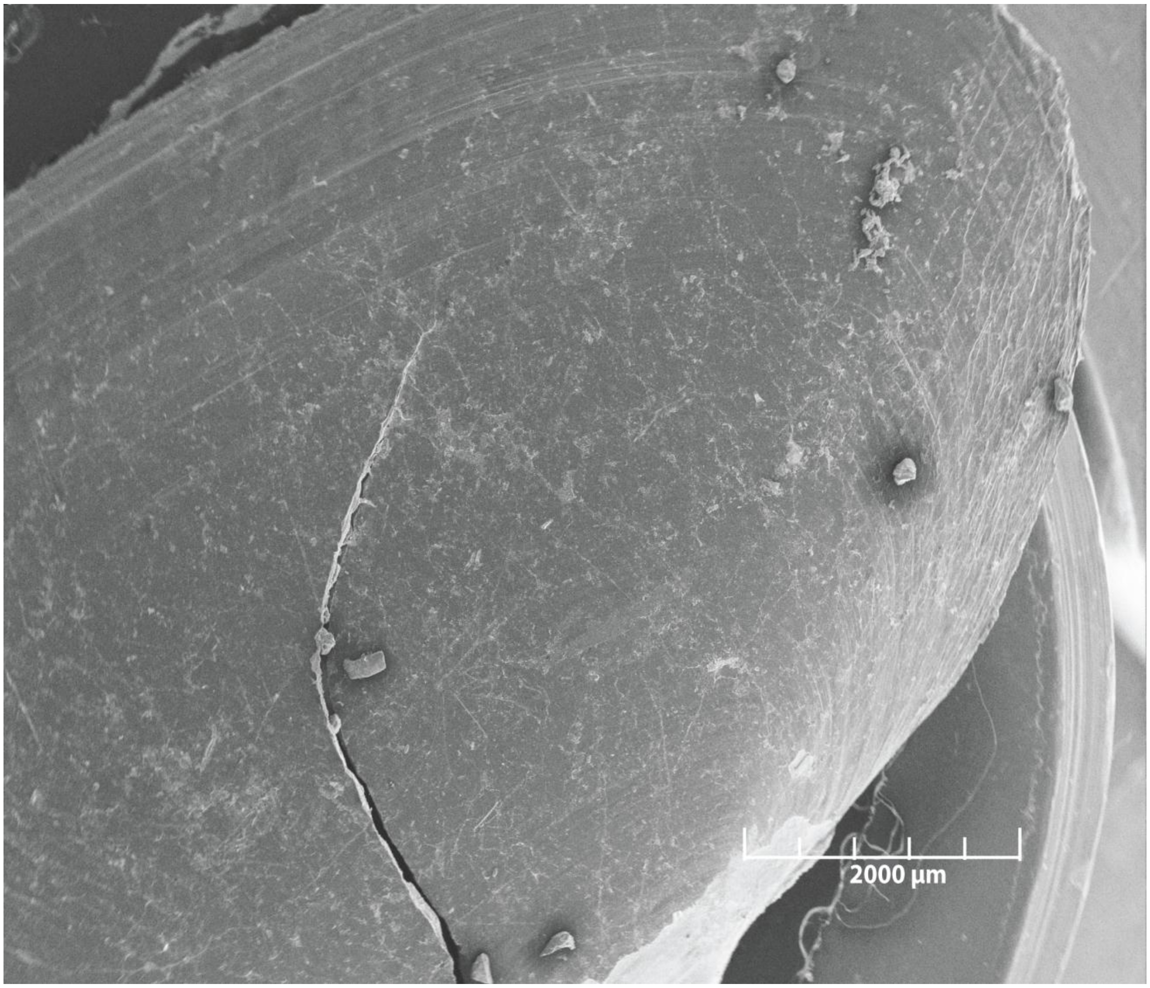

Figure A49, Macoma 11, 8 weeks

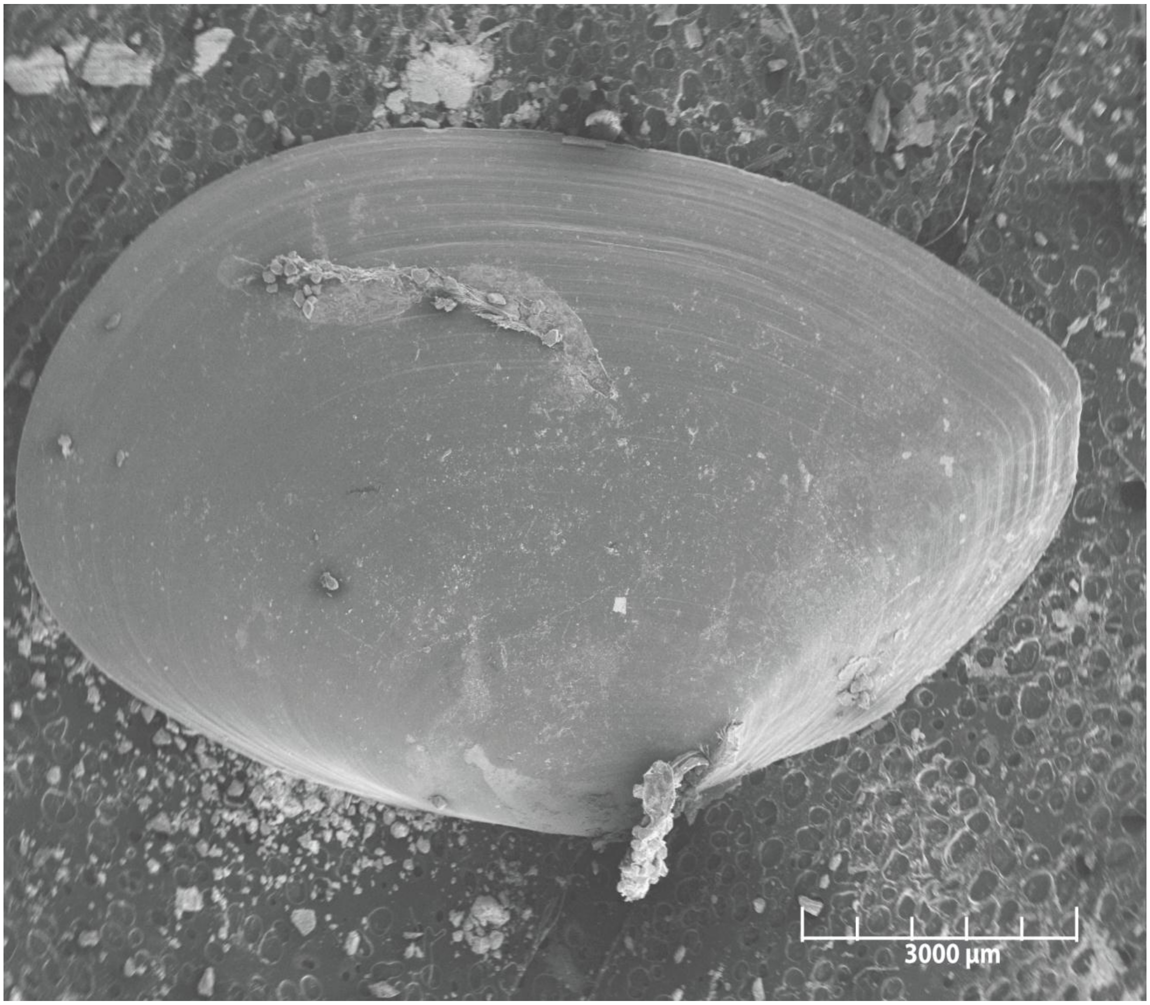

Figure A50, Macoma 12, 8 months

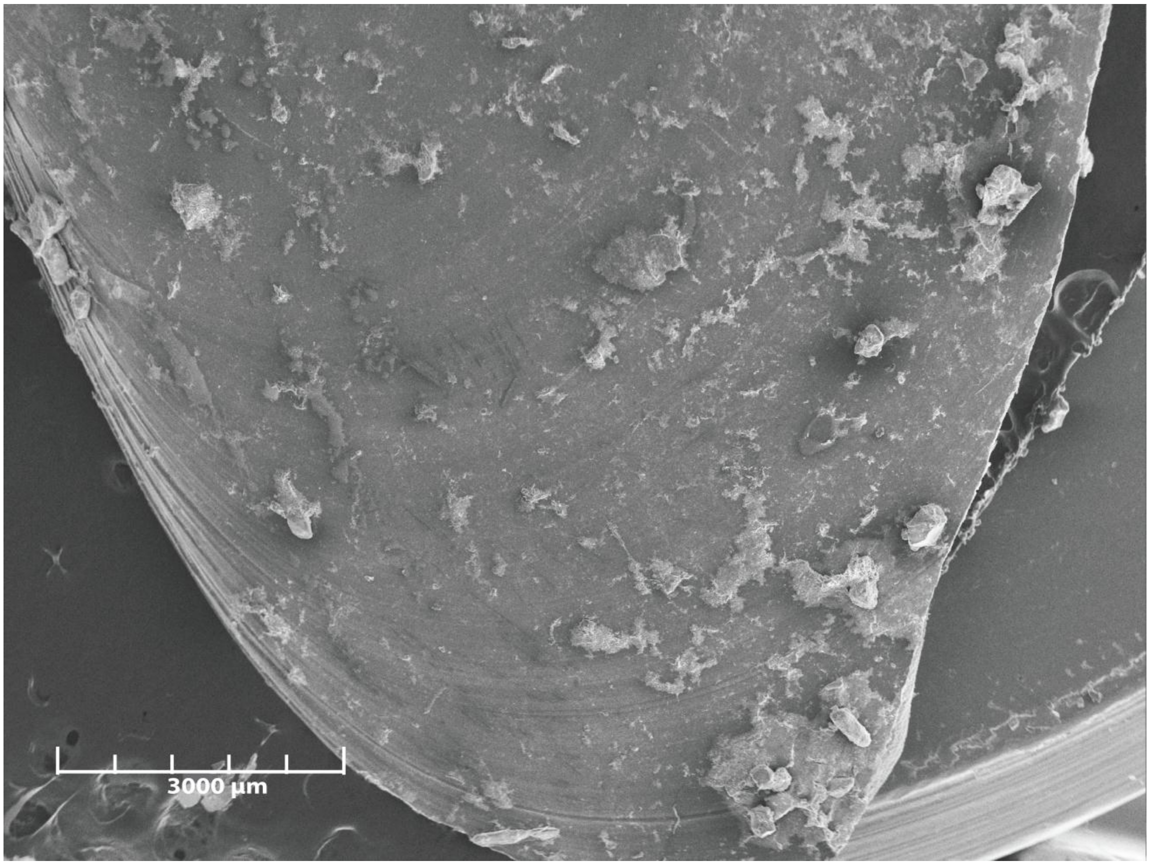

Figure A51, Macoma 14, 2 weeks

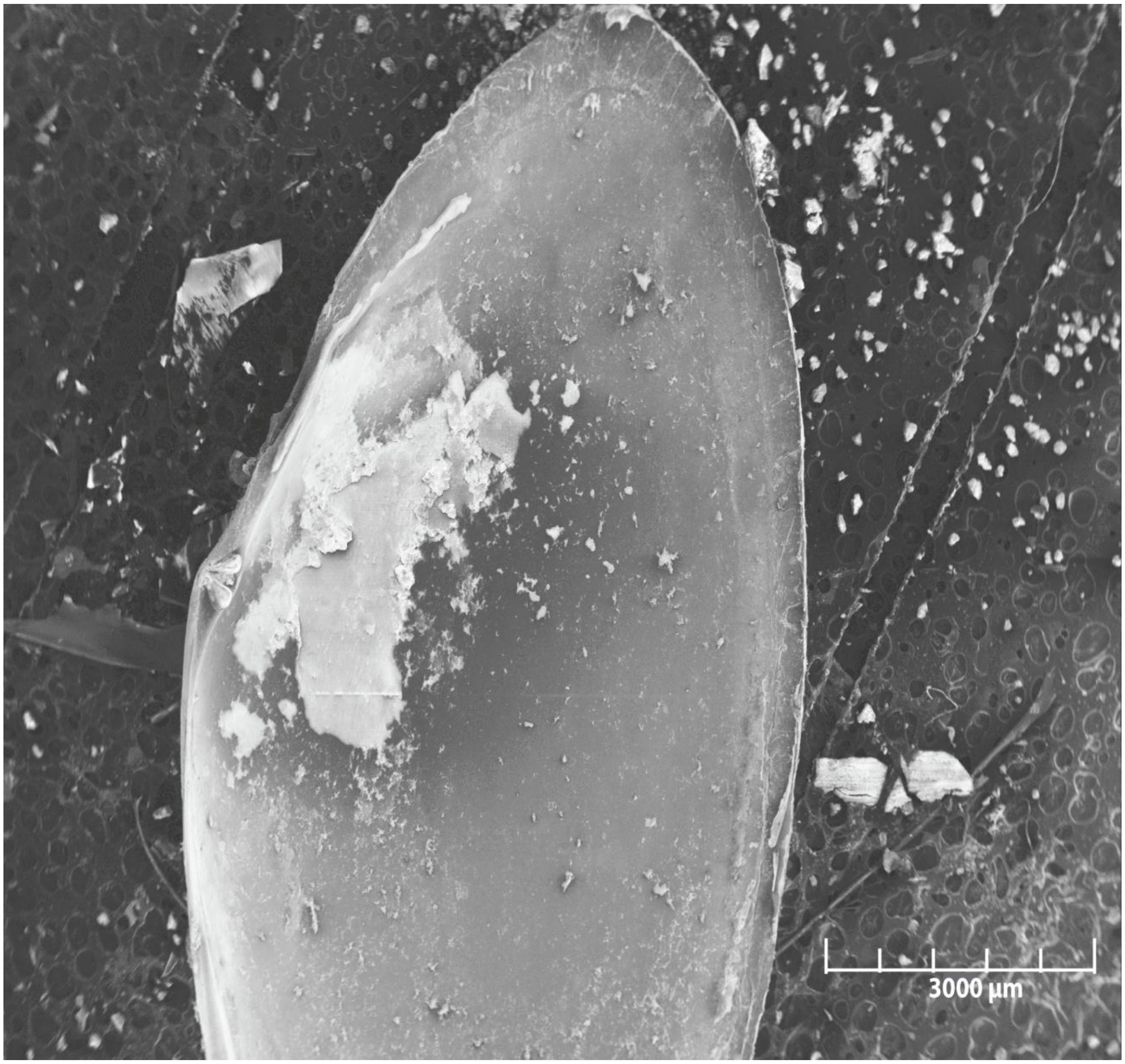

Figure A52, Macoma 15, 4 months

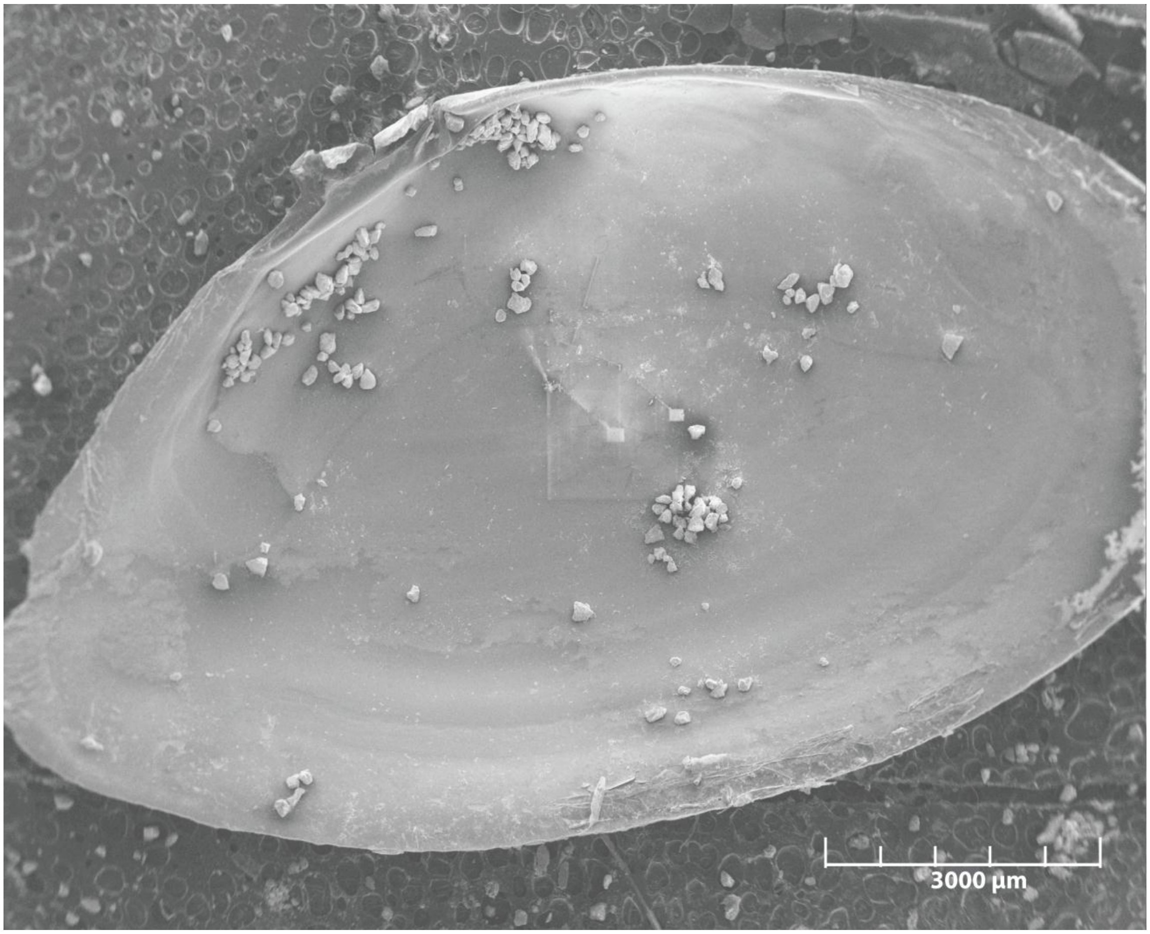

Figure A53, Macoma 16, 4 months

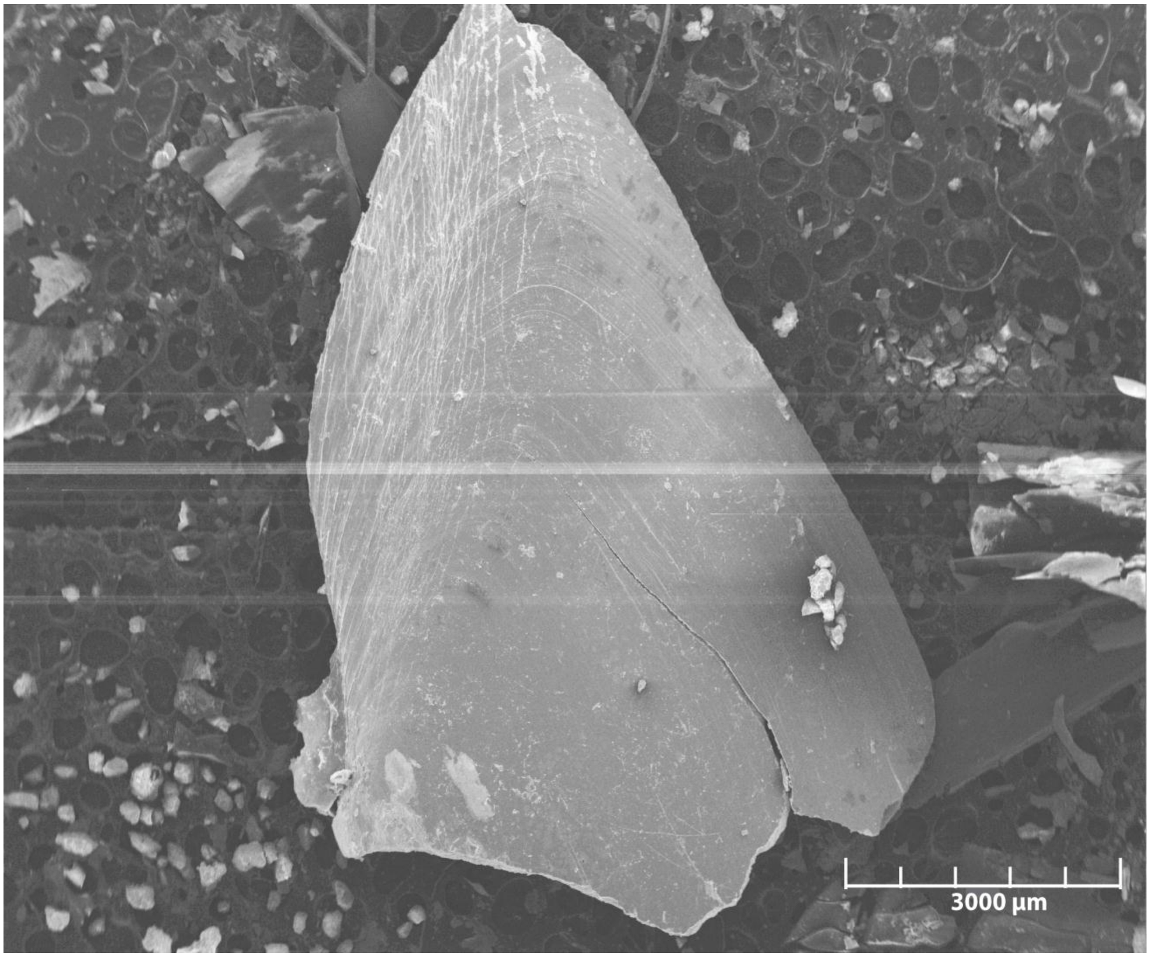

Figure A54, Macoma 18, 8 months

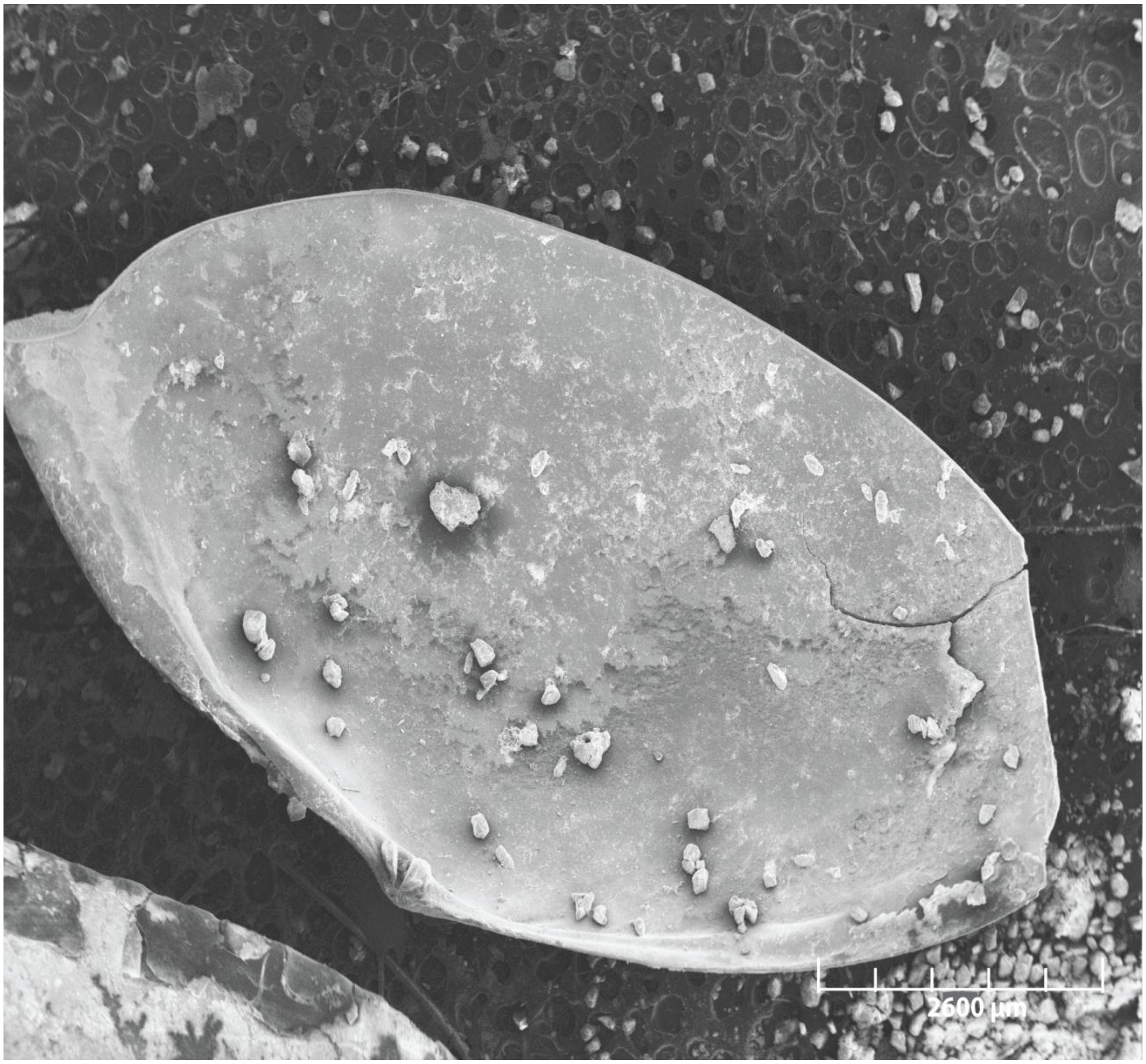

Figure A55, Macoma 19, 1 year

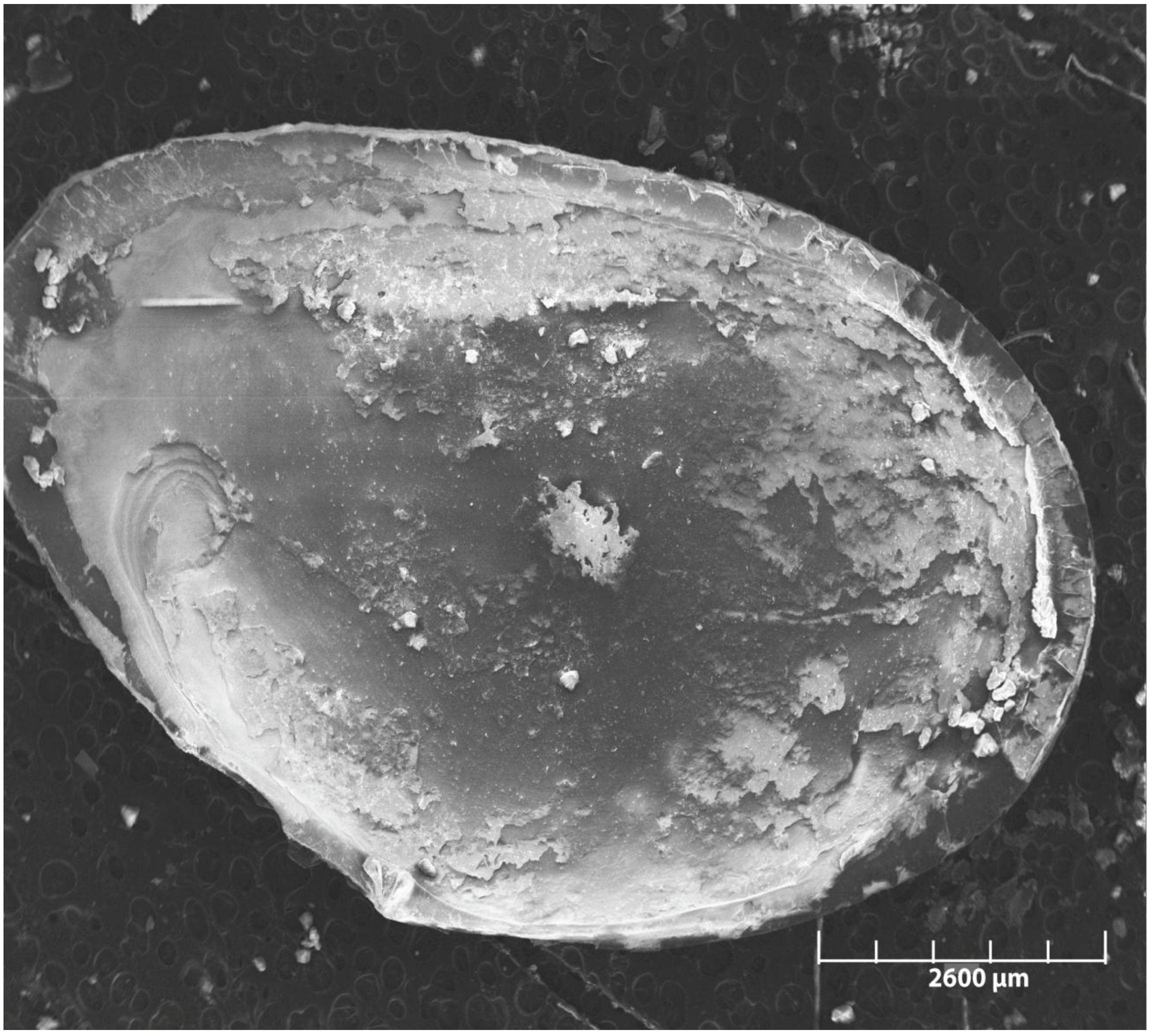

Figure A56, Macoma 24, 2 weeks

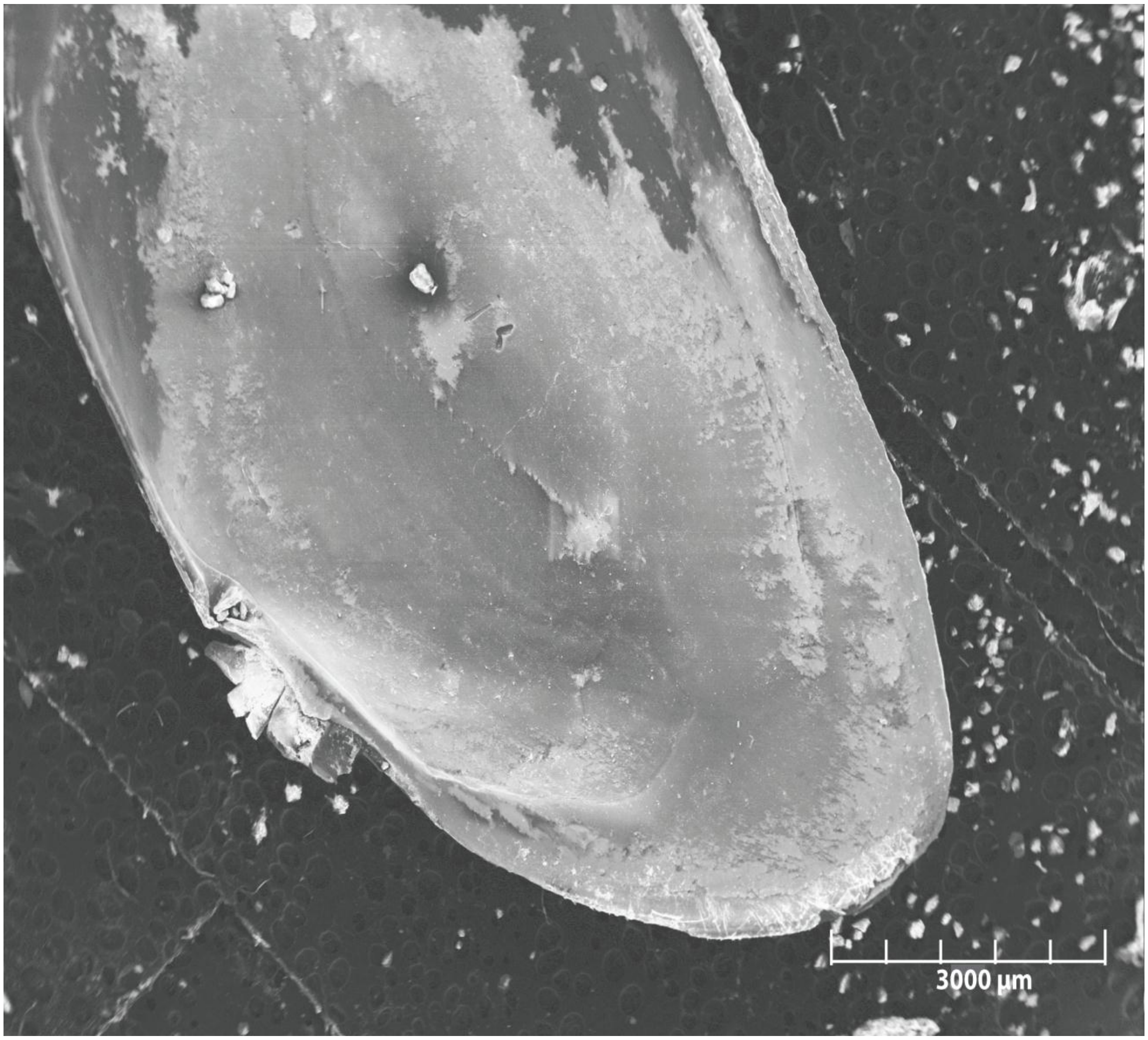

Figure A57, Macoma 25, 4 weeks

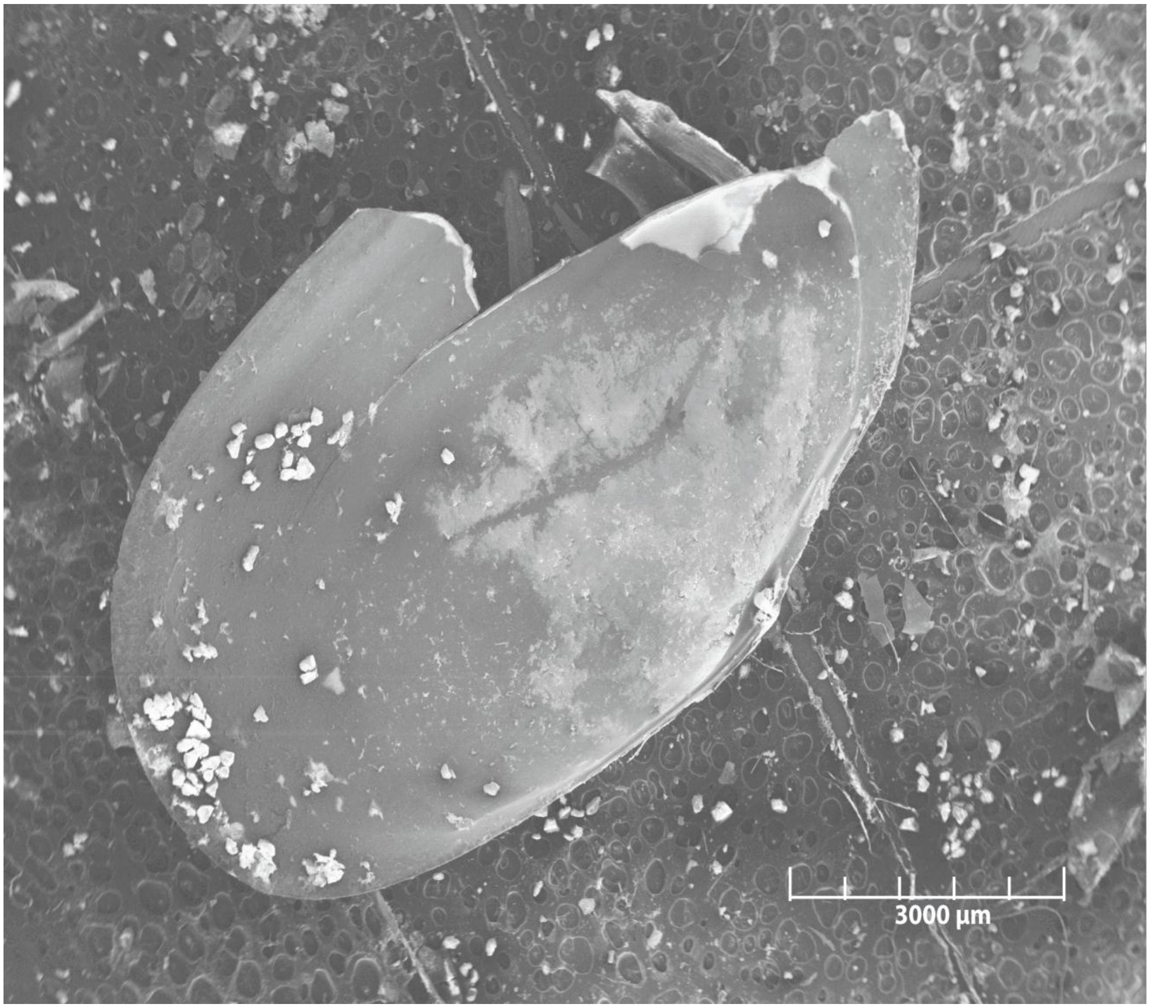

Figure A58, Macoma 26, 8 weeks

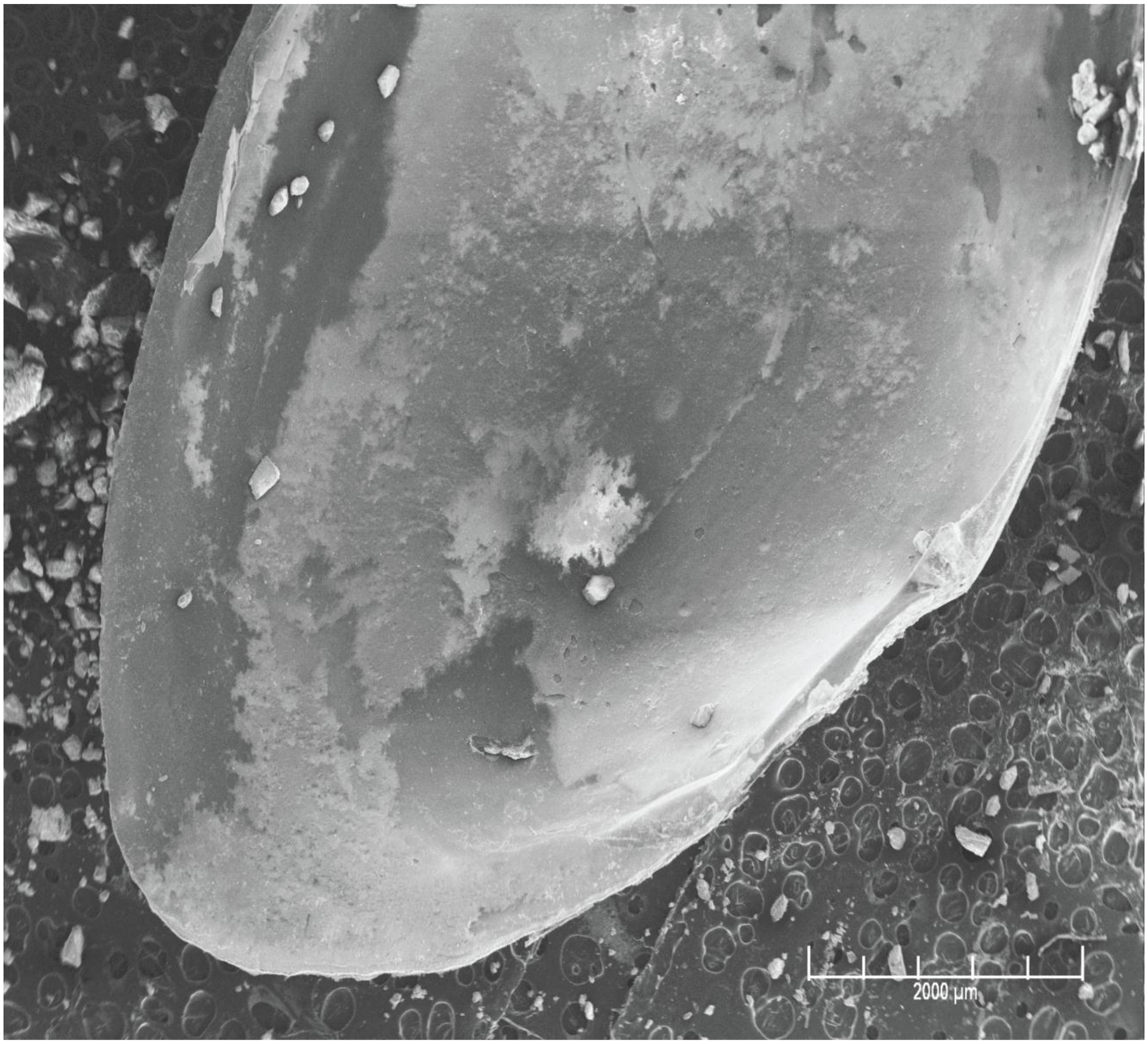

Figure A59, Macoma 28, 4 months

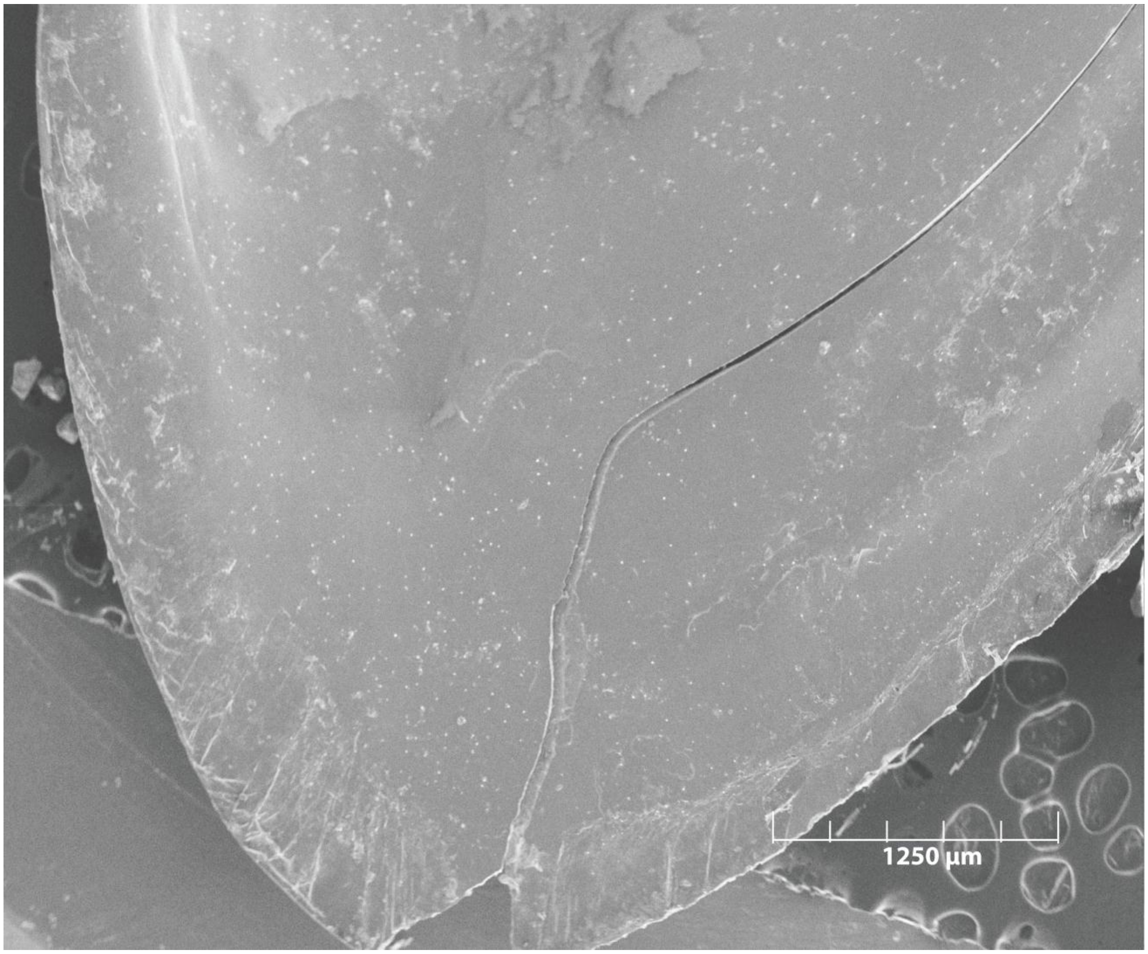

Figure A60, Macoma 29, 8 weeks

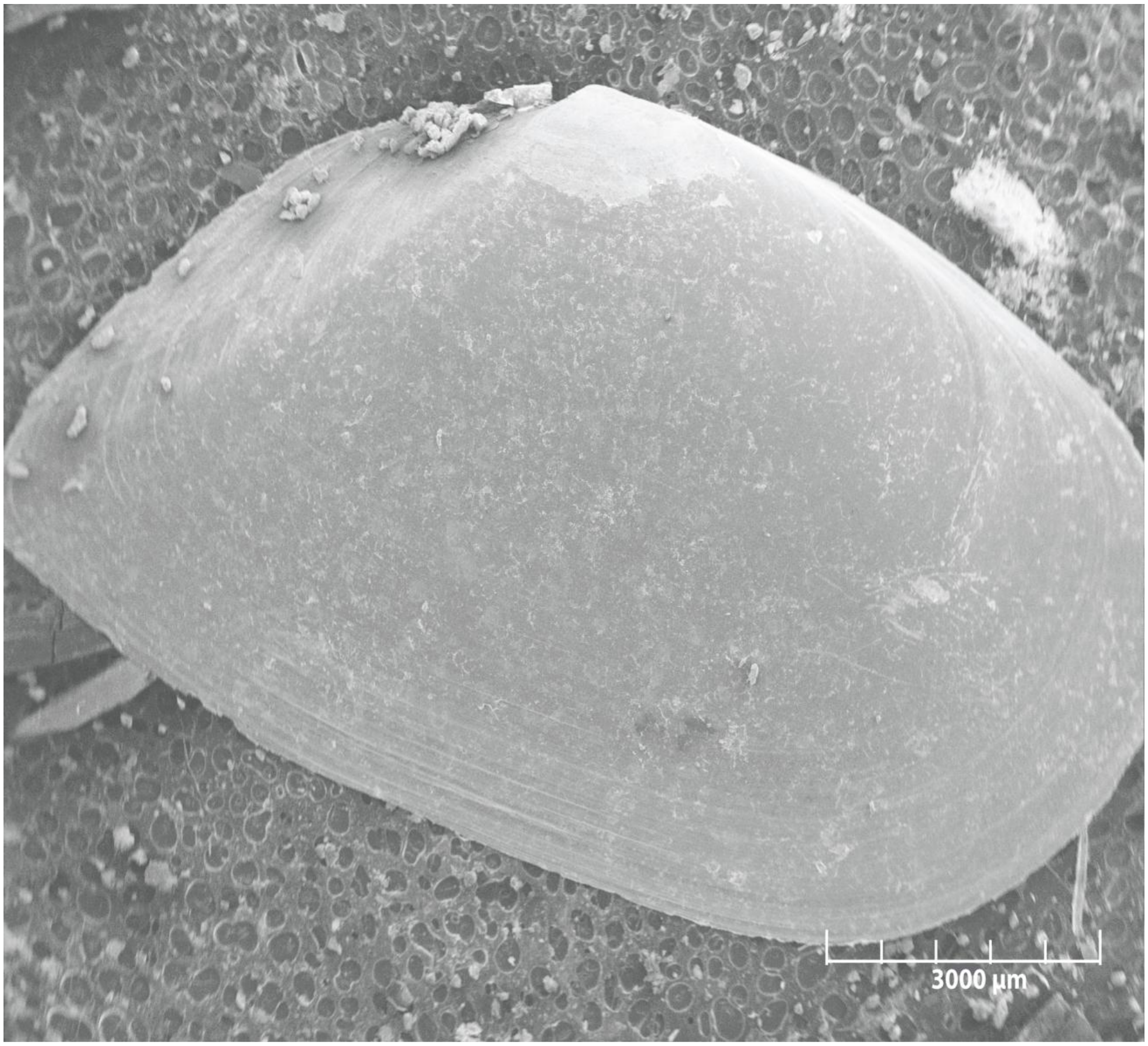

Figure A61, Macoma 30, 4 months

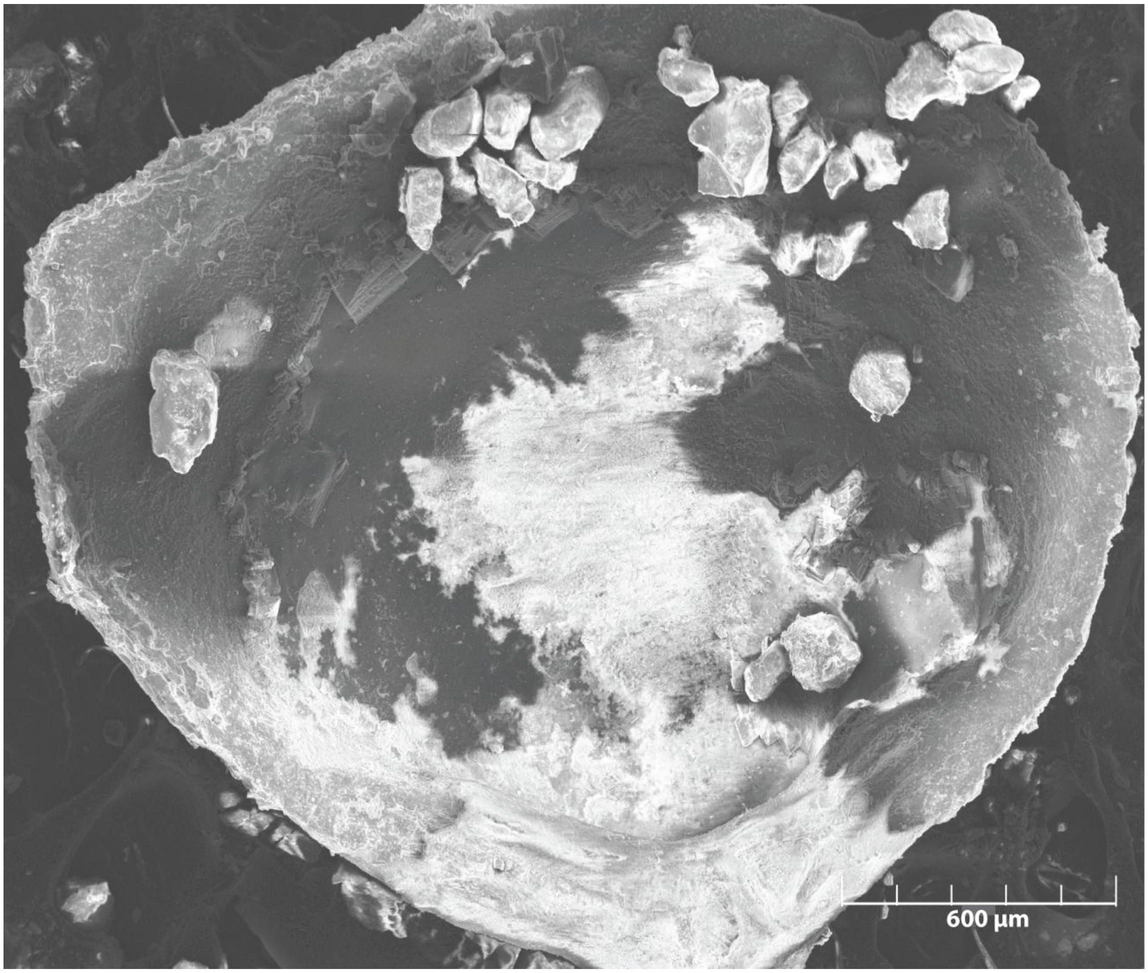

Figure A62, Mulinia 1, 1 year

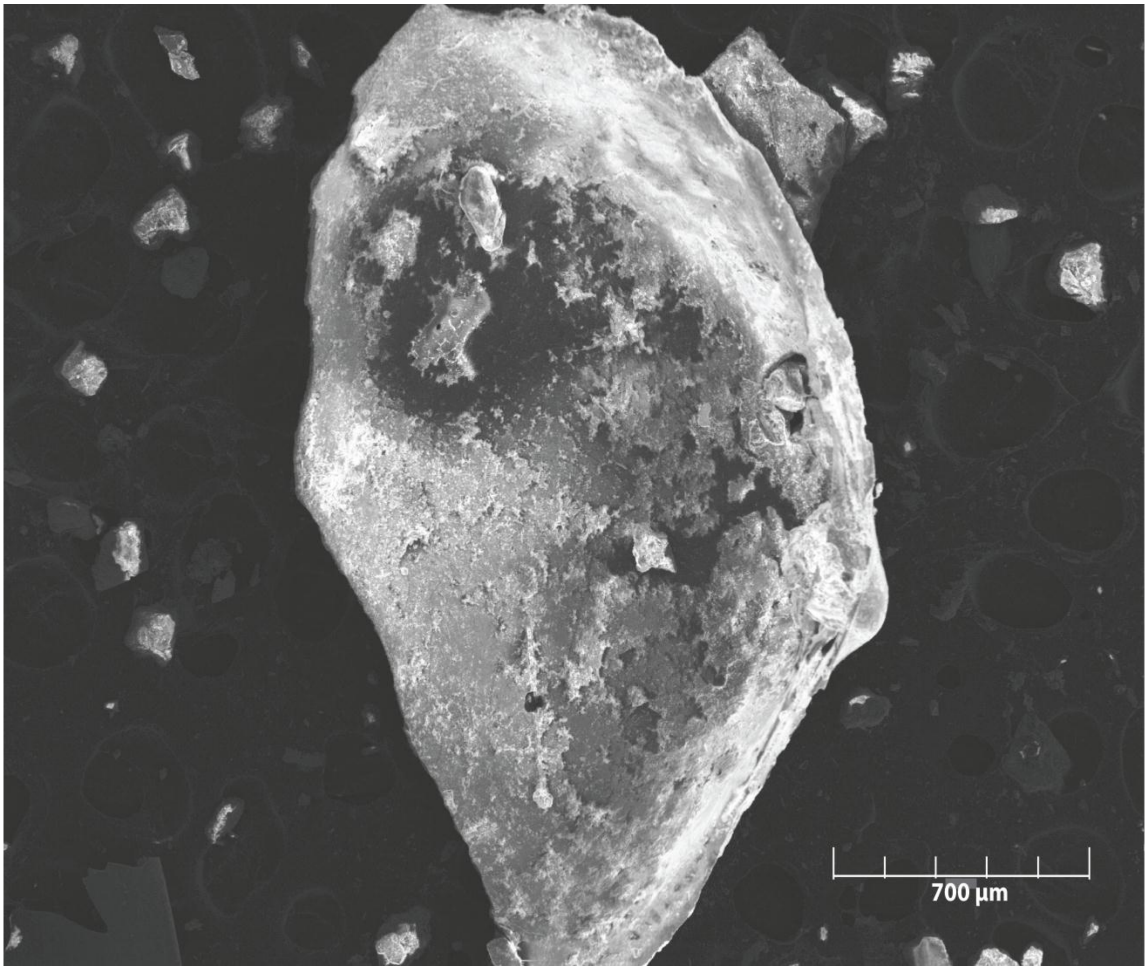

Figure A63, Mulinia 2, 1 year

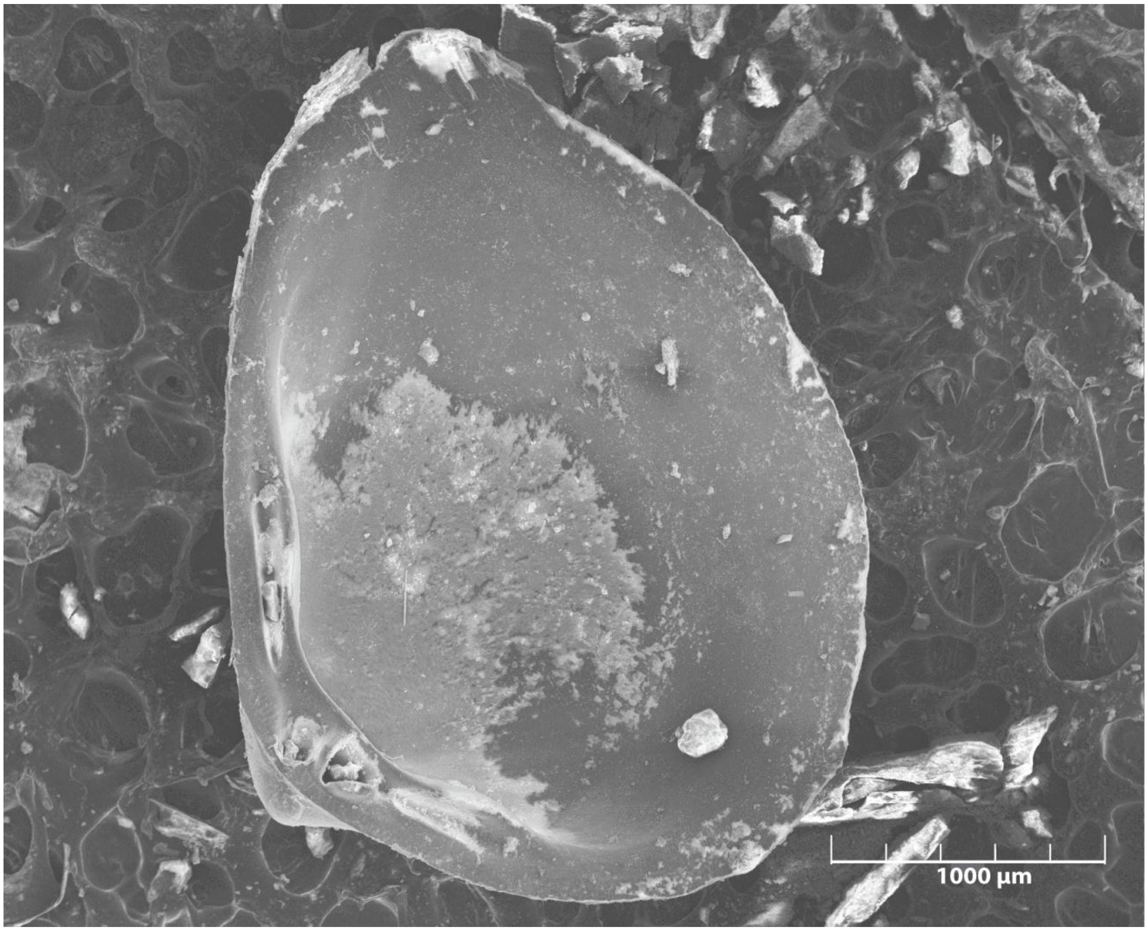

Figure A64, Mulinia 3, 4 months

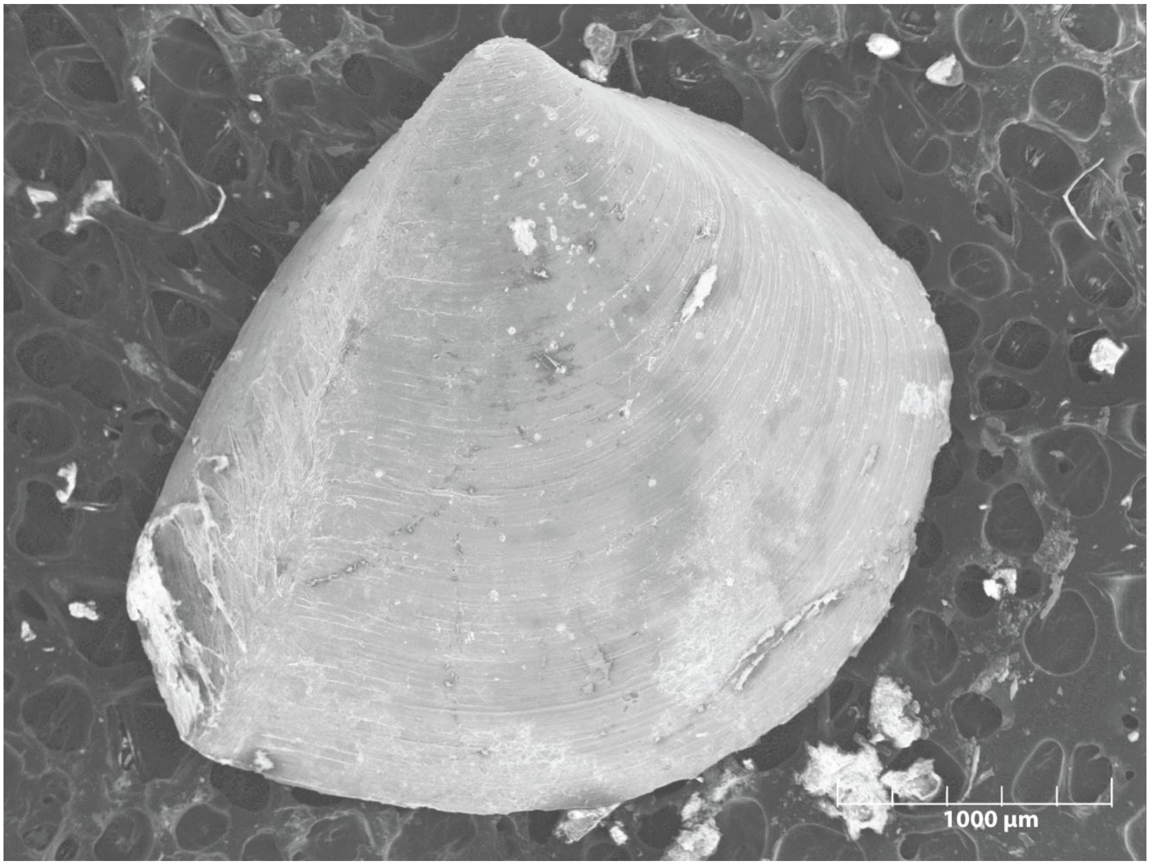

Figure A65, Mulinia 4, 4 weeks

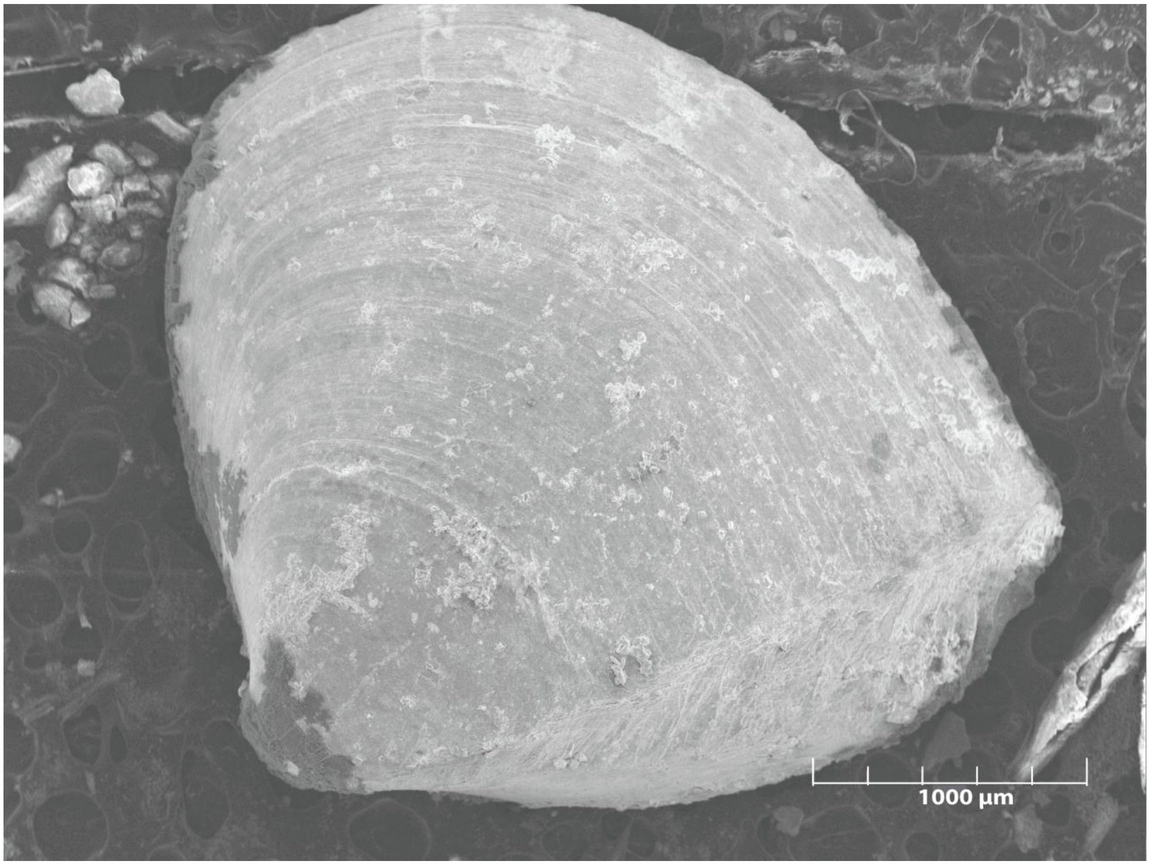

Figure A66, Mulinia 7, 8 months

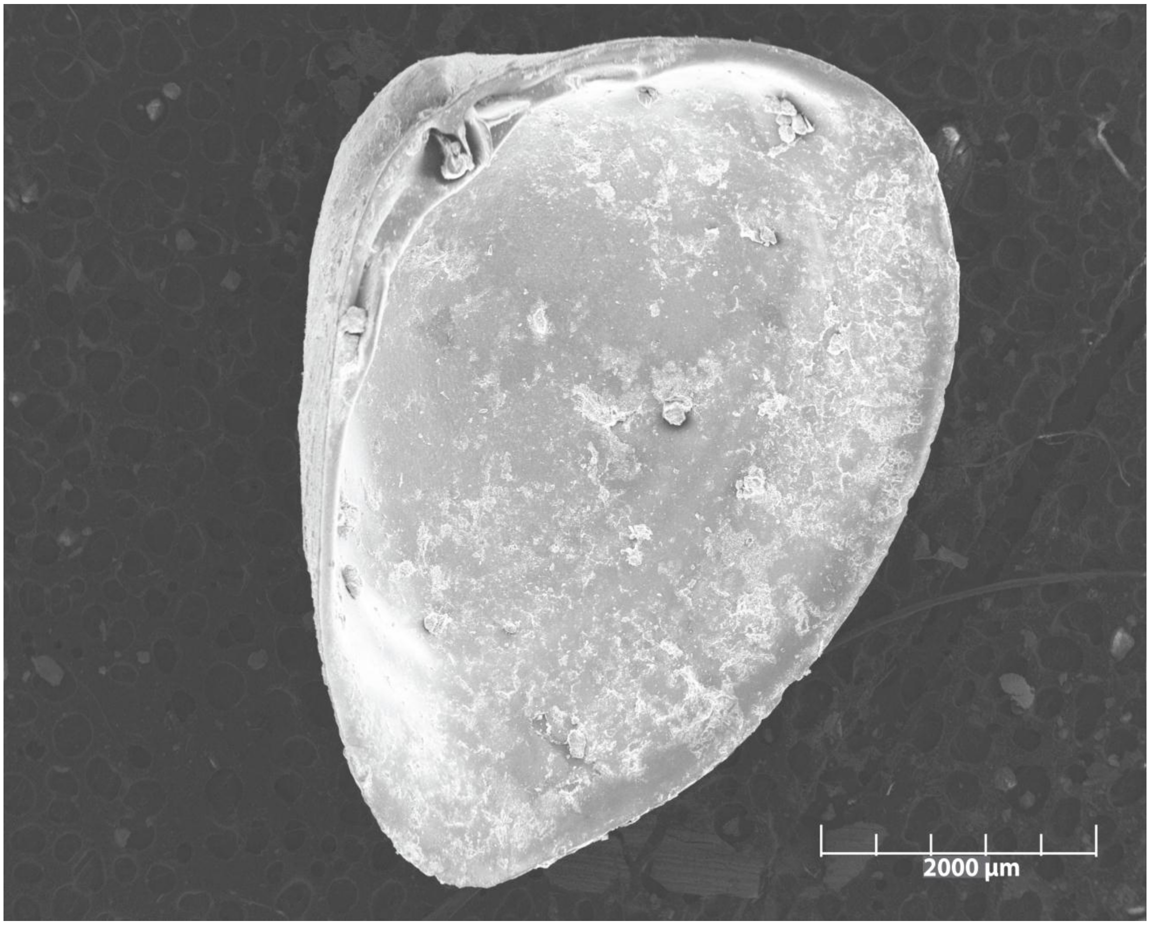

Figure A67, Mulinia 10, 8 months

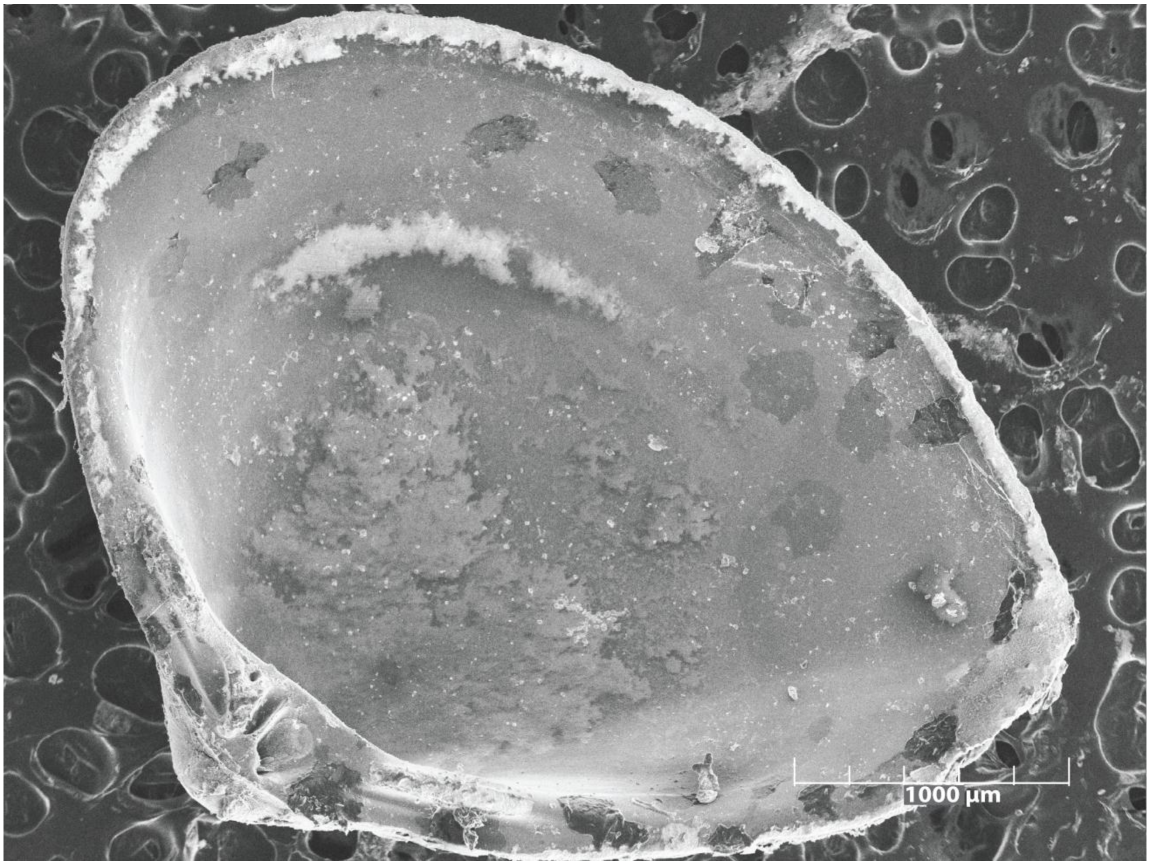

Figure A68, Mulinia 12, 8 weeks

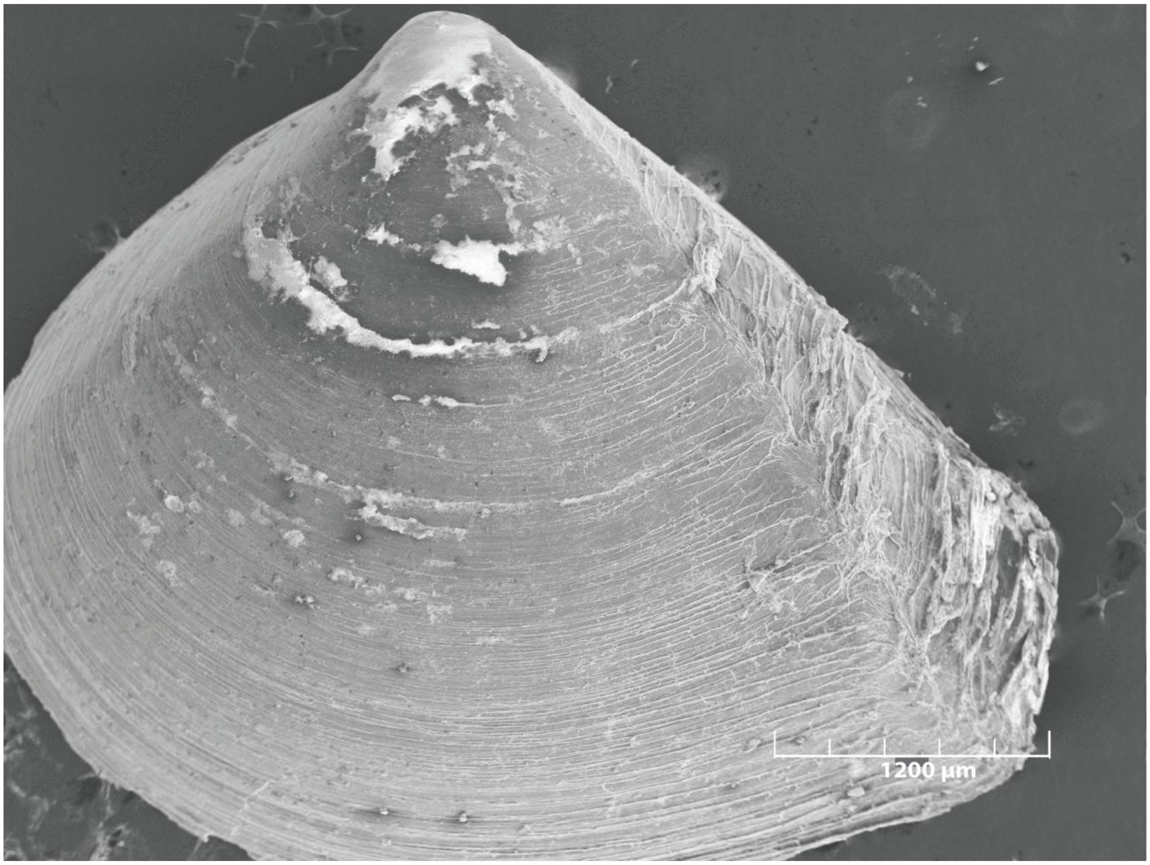

Figure A69, Mulinia 14, 8 weeks

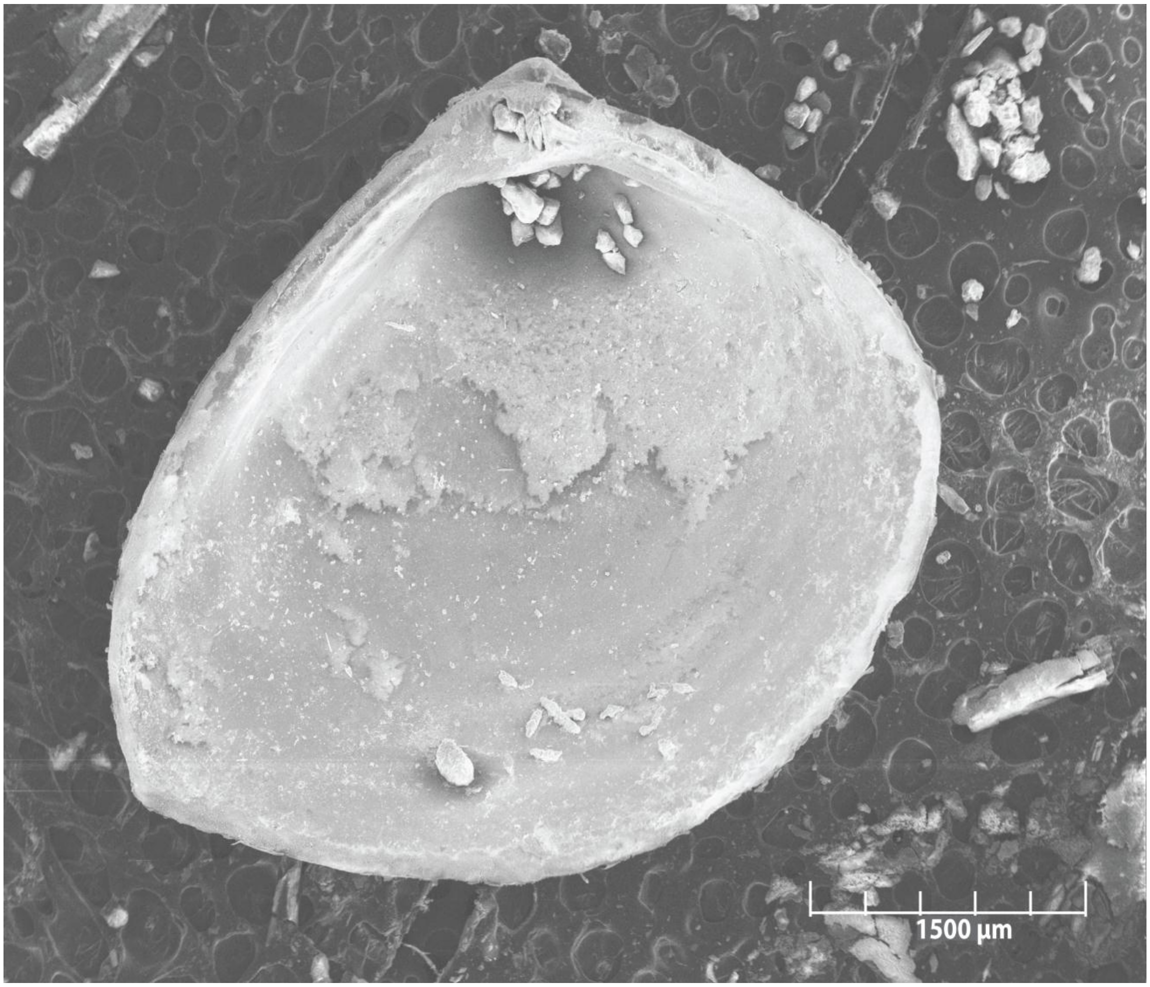

Figure A70, Mulinia 16, 4 months

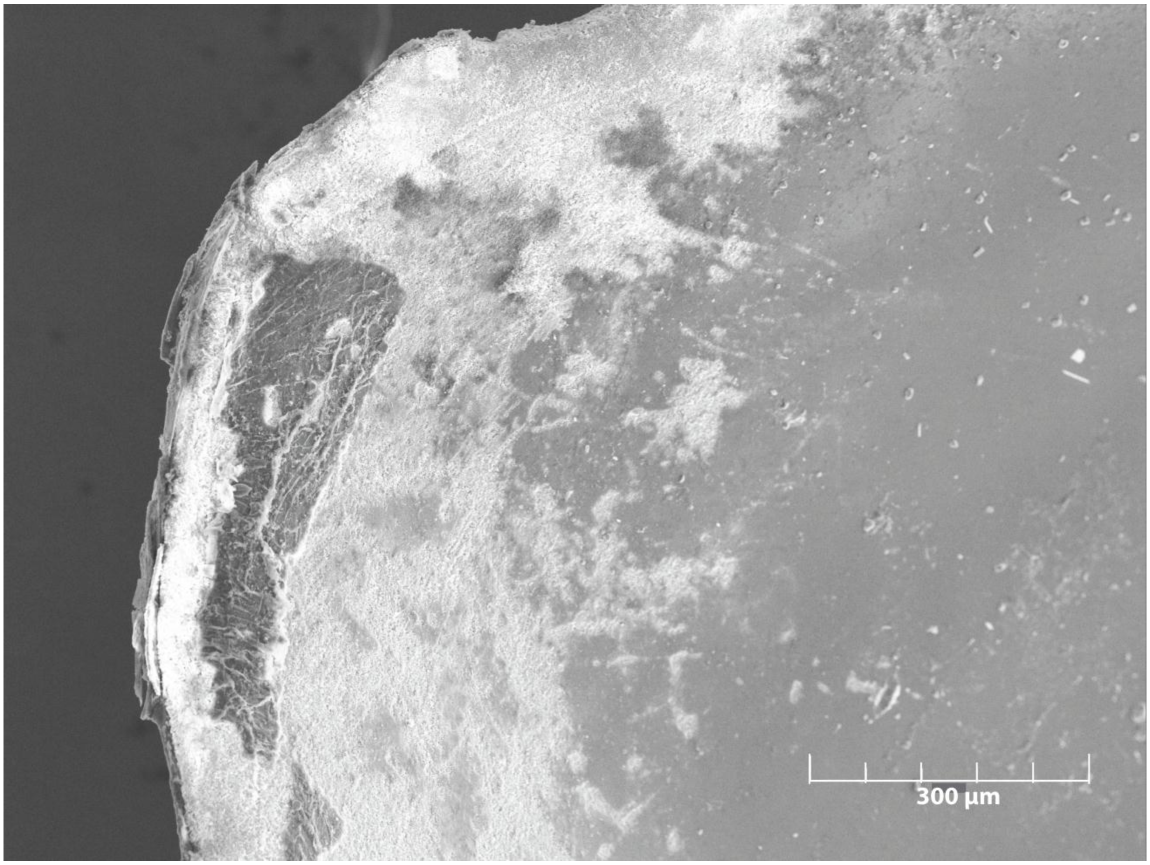

Figure A71, Mulinia 17, 4 weeks

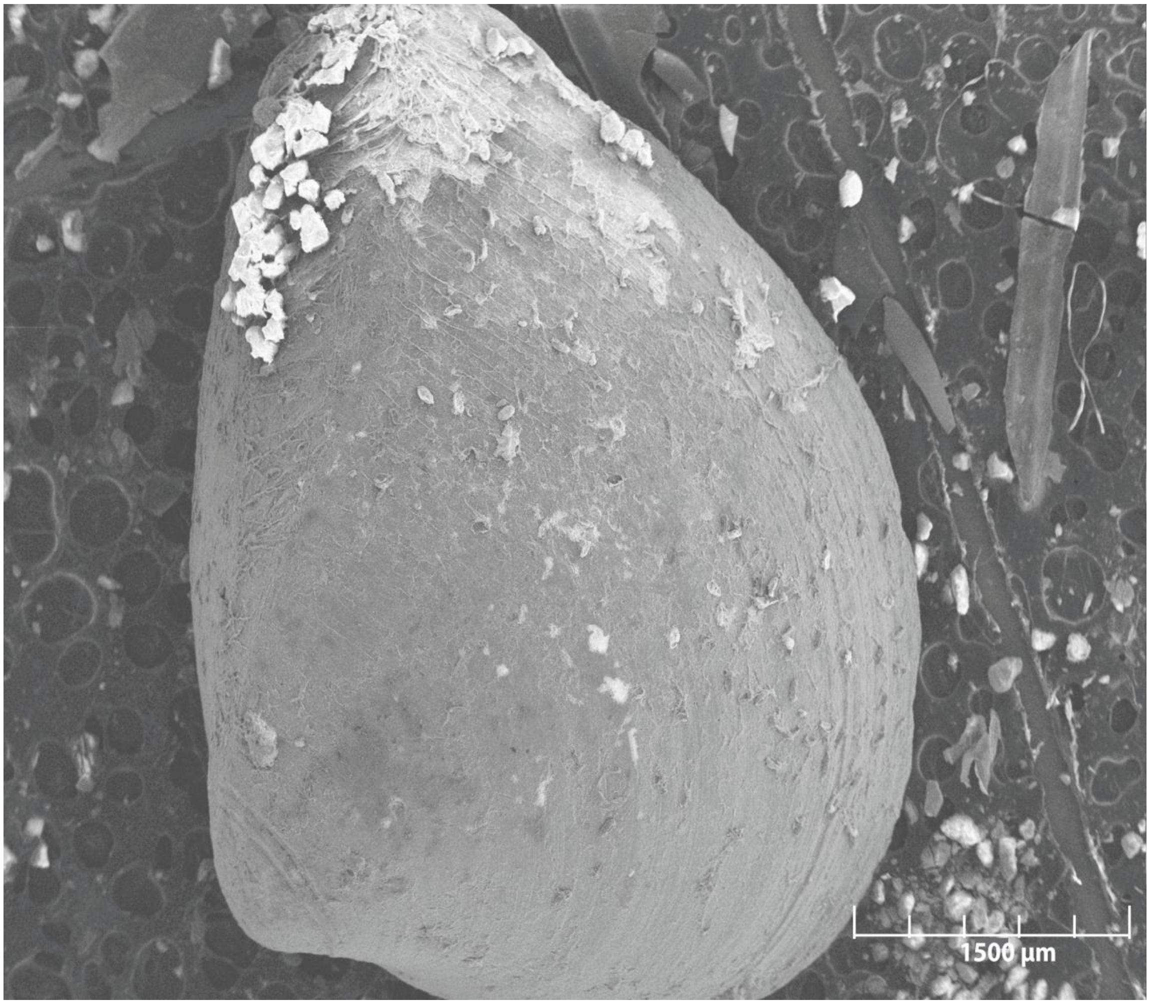

Figure A72, Mulinia 19, 4 months

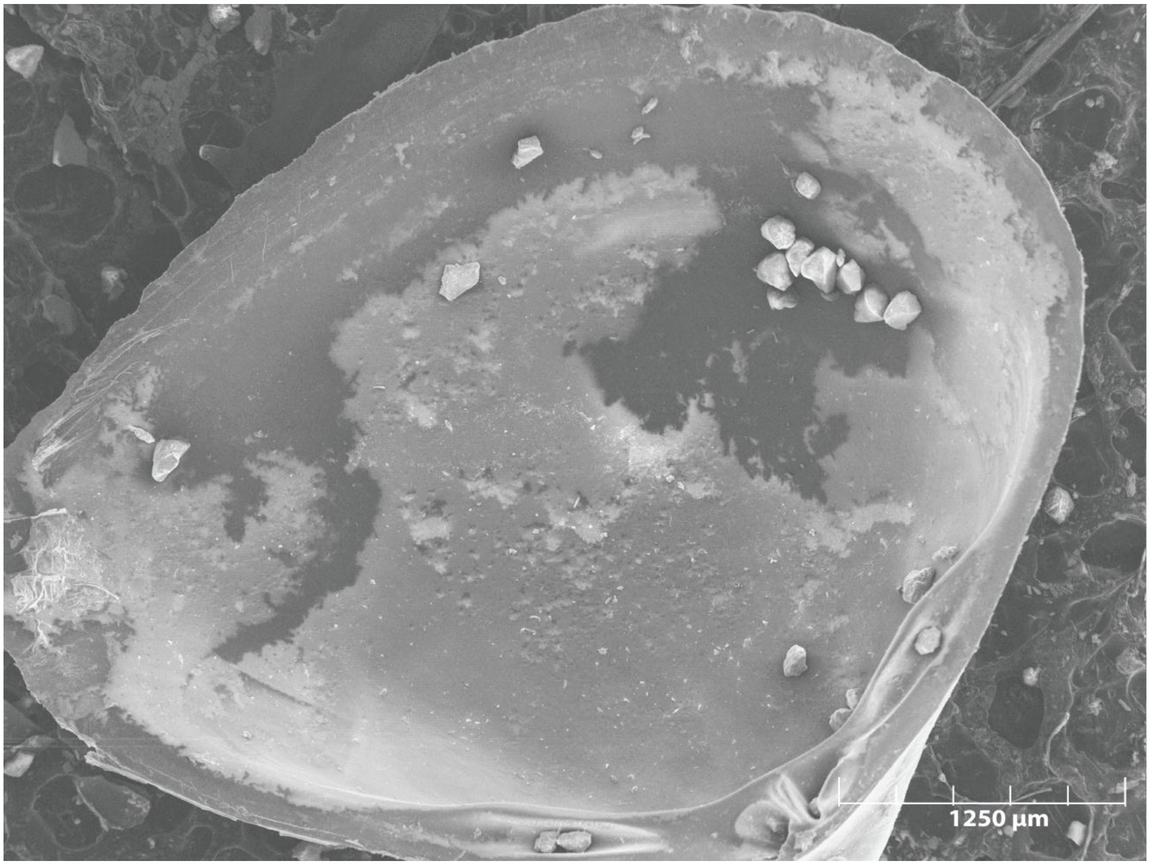

Figure A73, Mulinia 20, 4 months

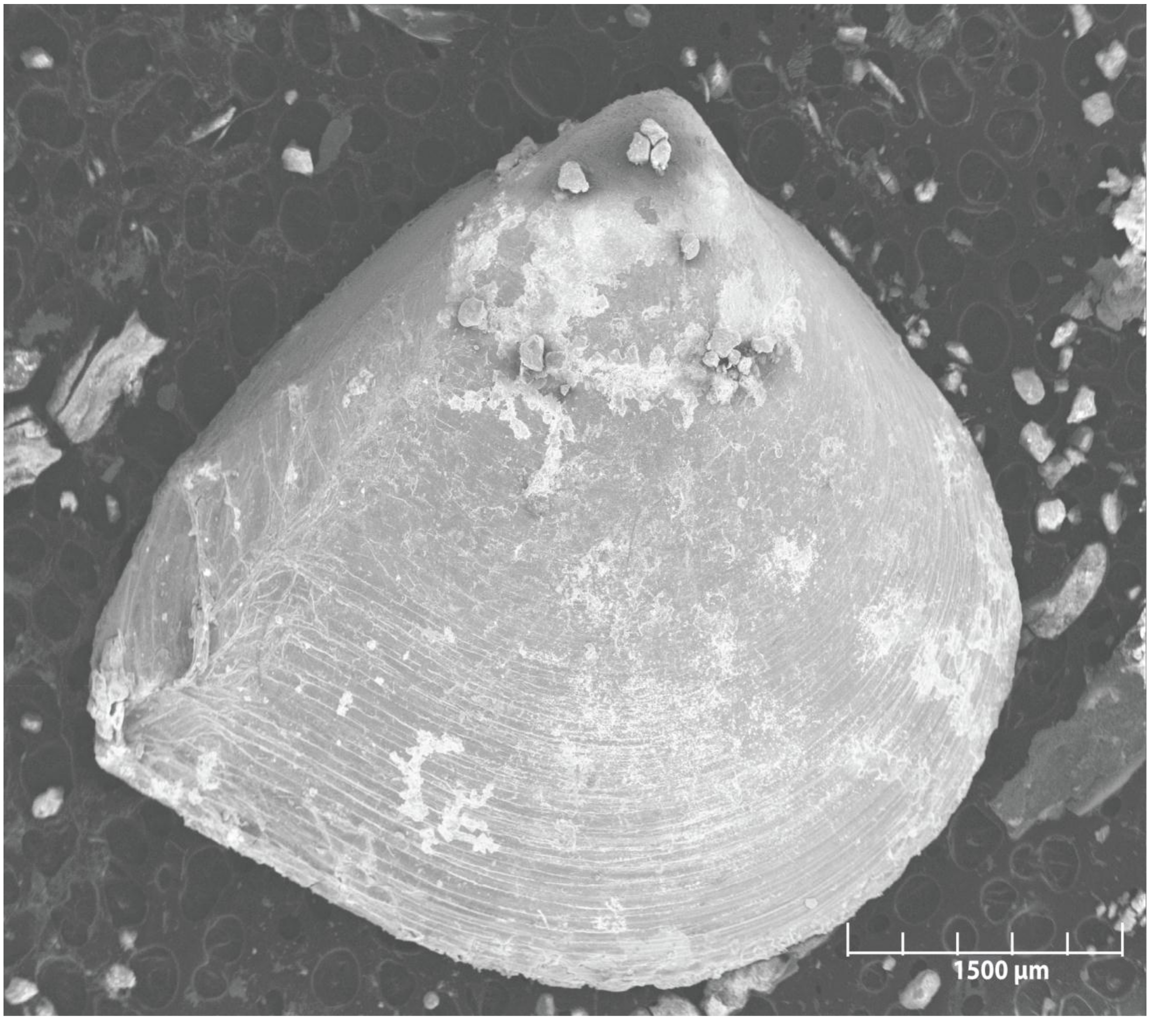

Figure A74, Mulinia 21, 1 year

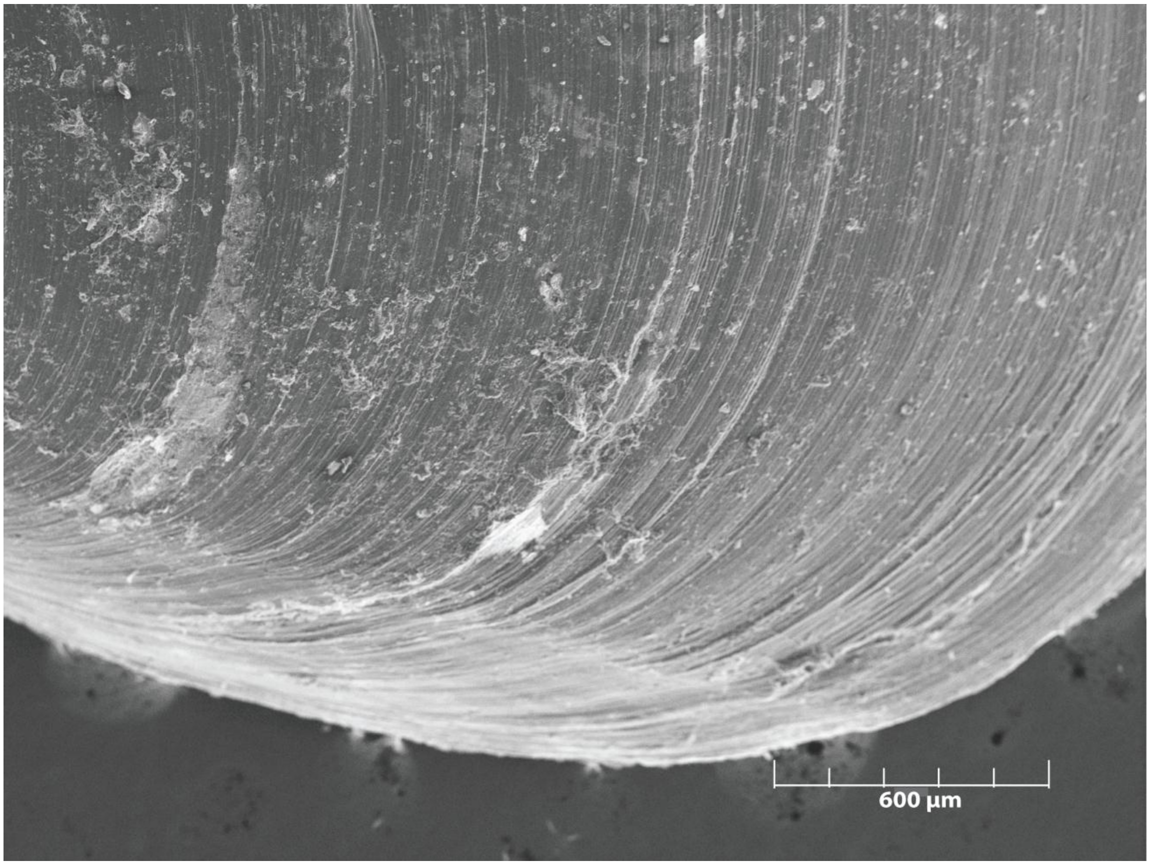

Figure A75, Mulinia 22, 8 weeks

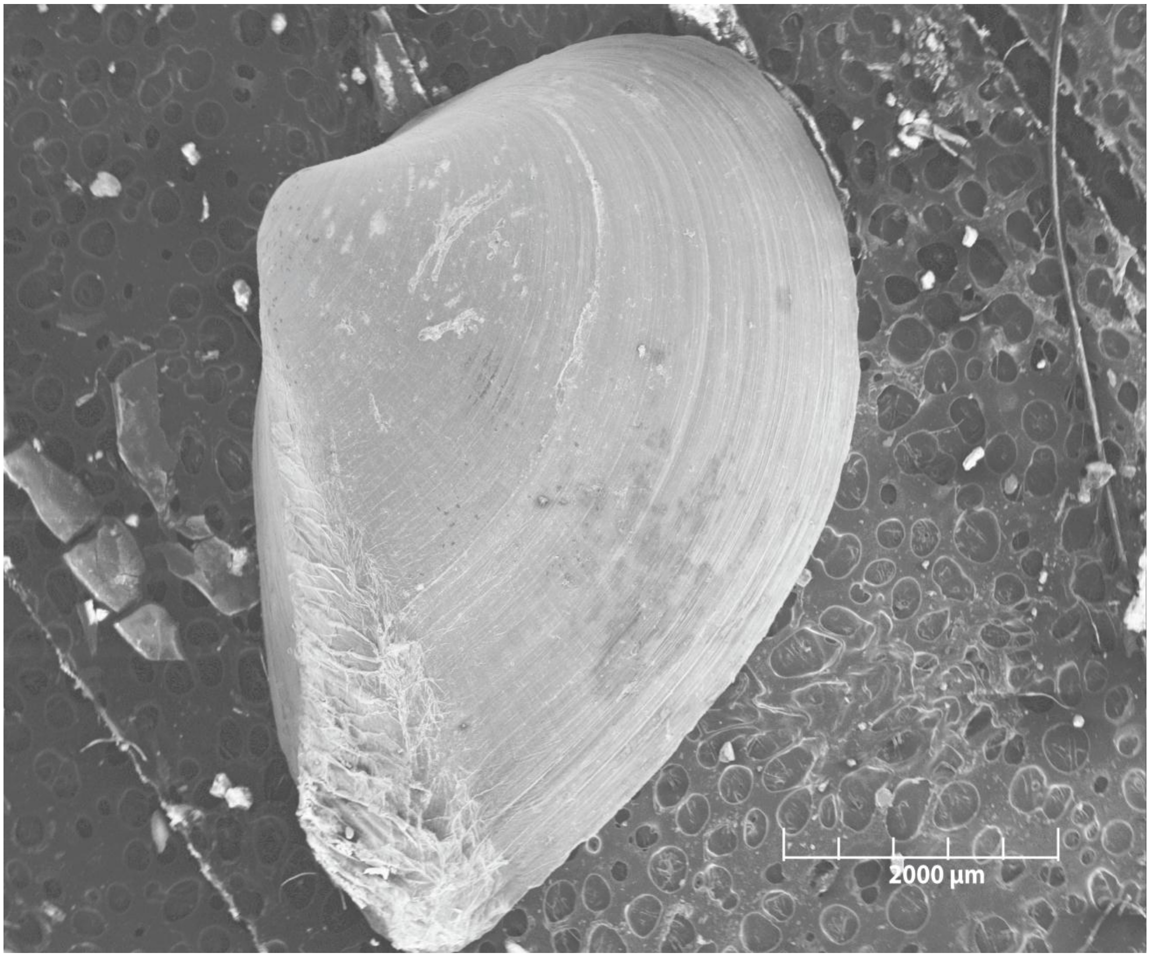

Figure A76, Mulinia 24, 4 weeks

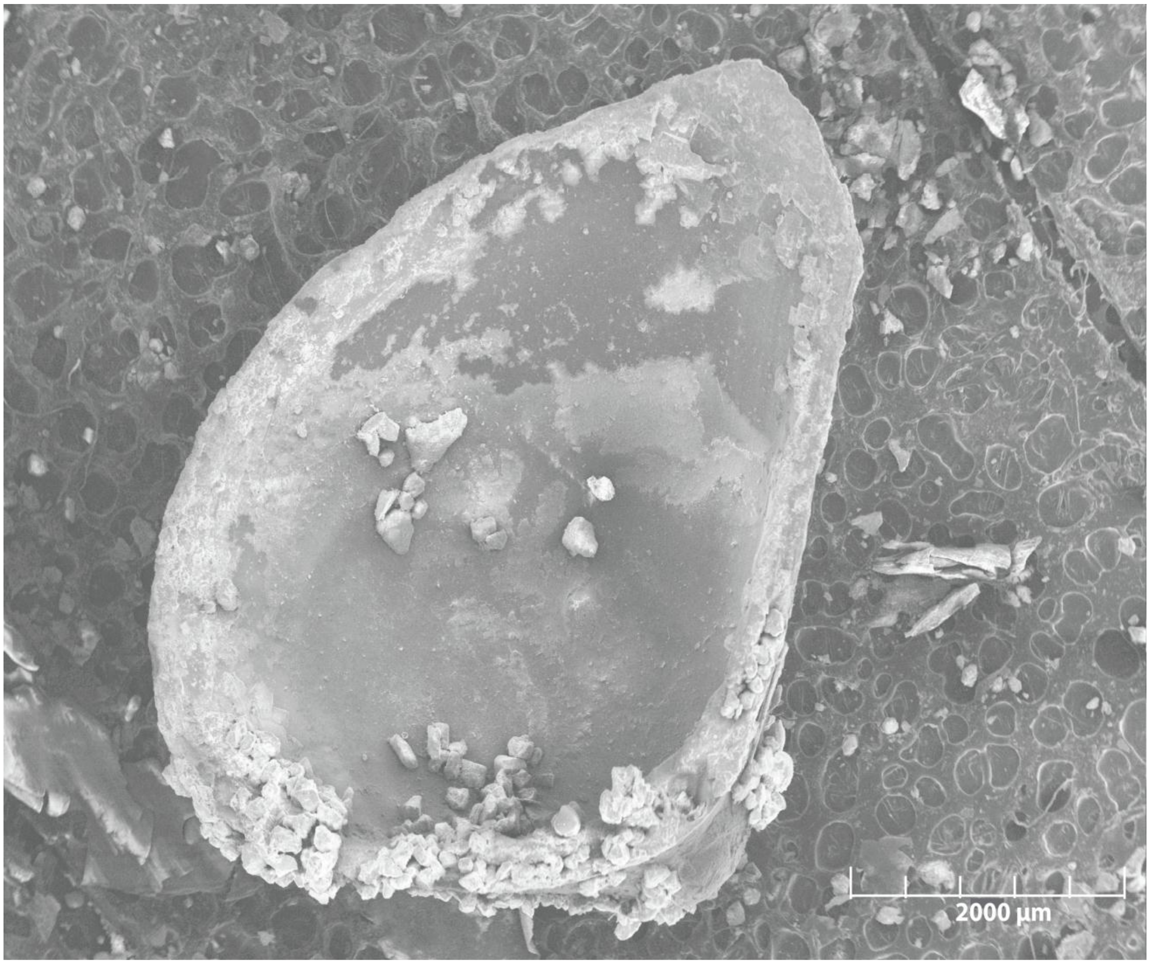

Figure A77, Mulinia 26, 1 year

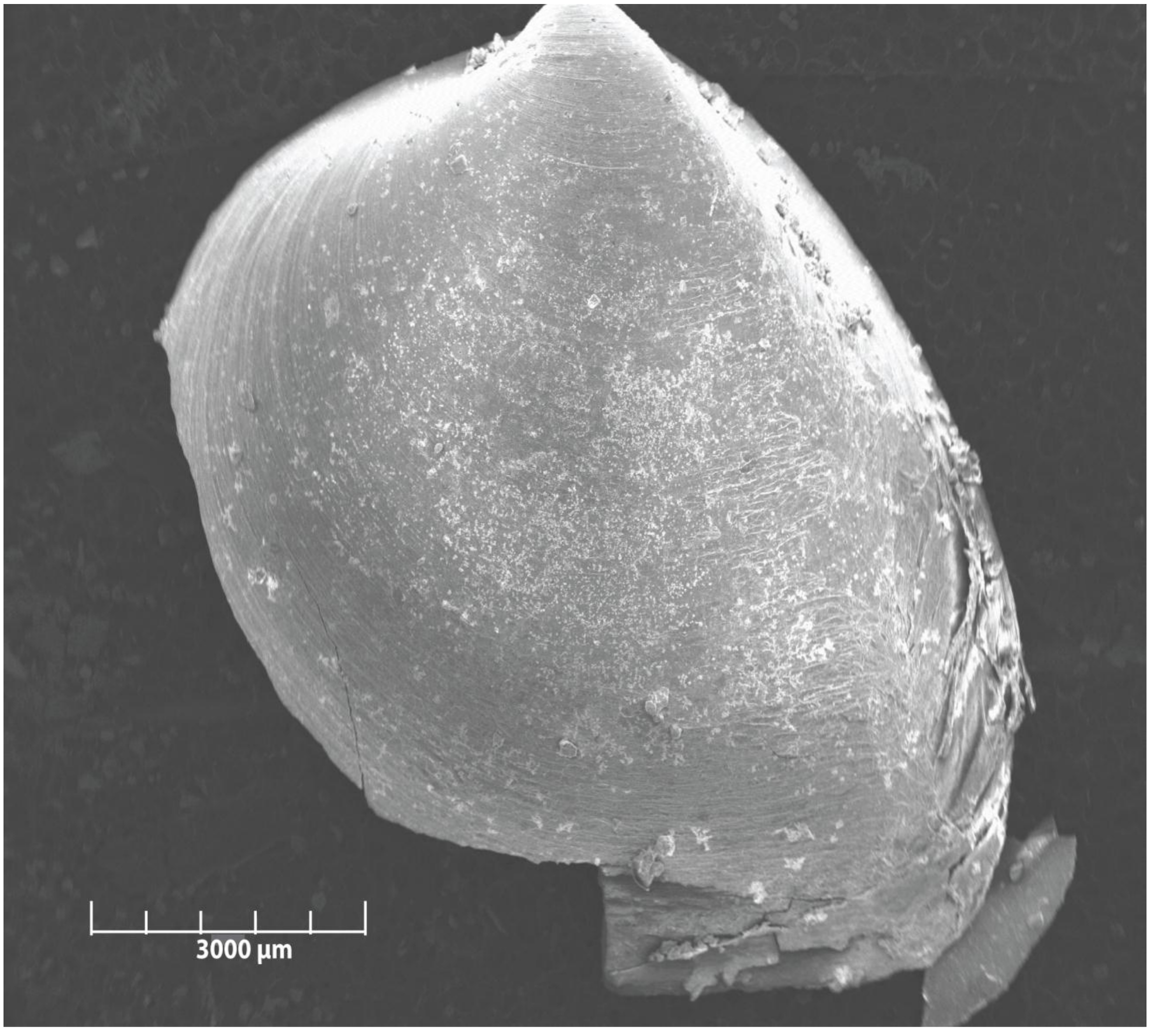

Figure A78, Mulinia 28, 8 months

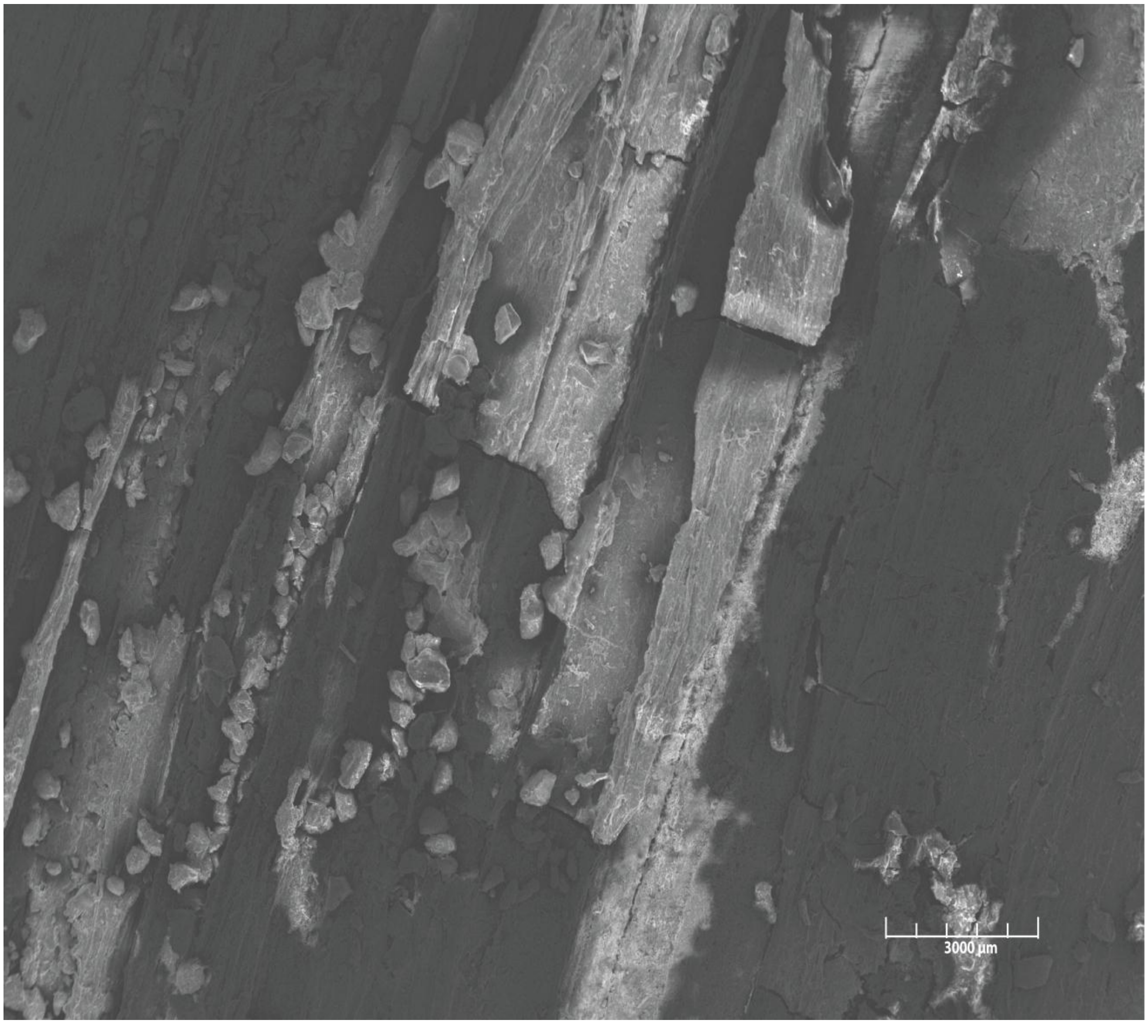

Figure A79, Mulinia 1, 2weeks

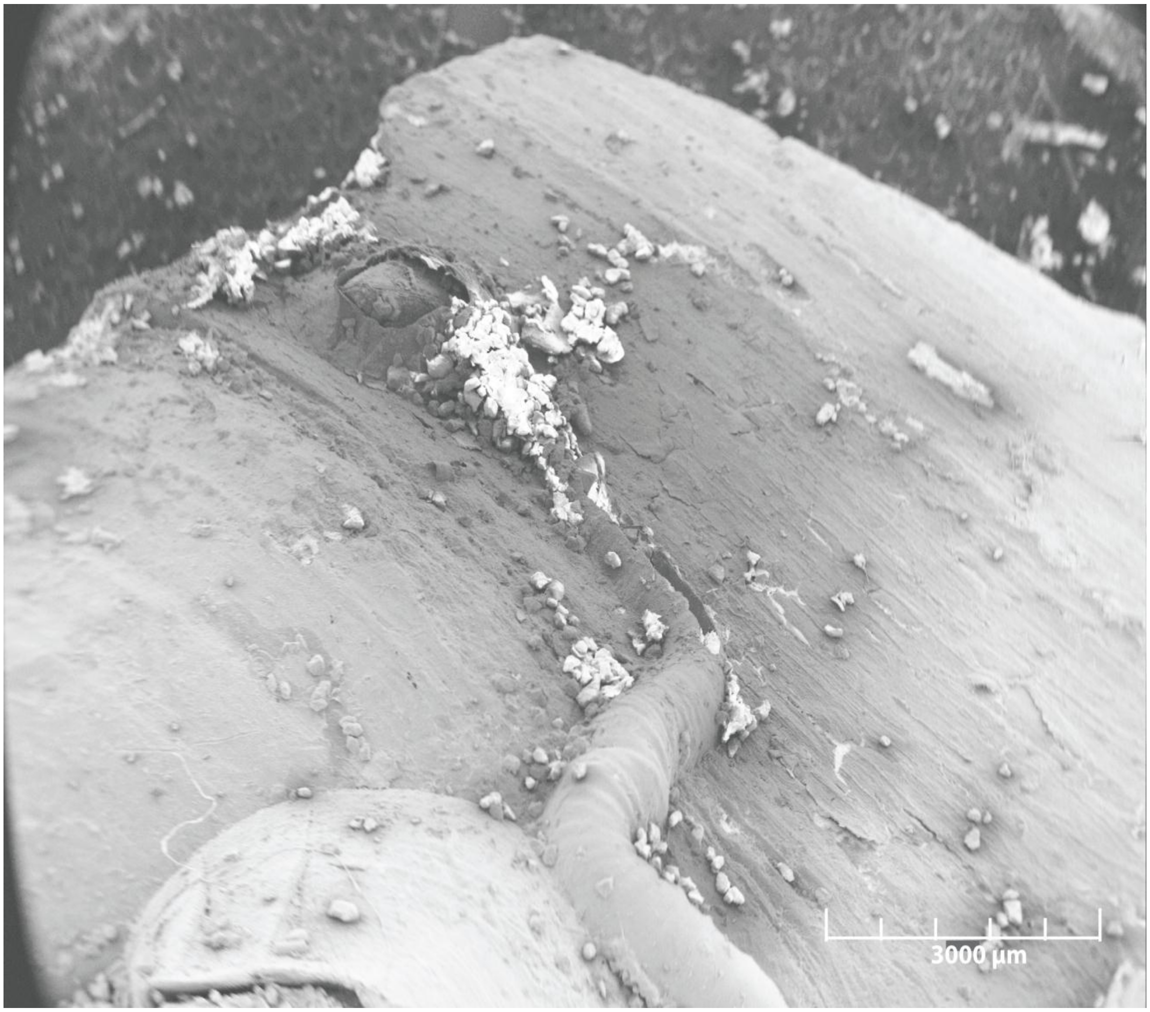

Figure A80, Rangia 1, 4 months

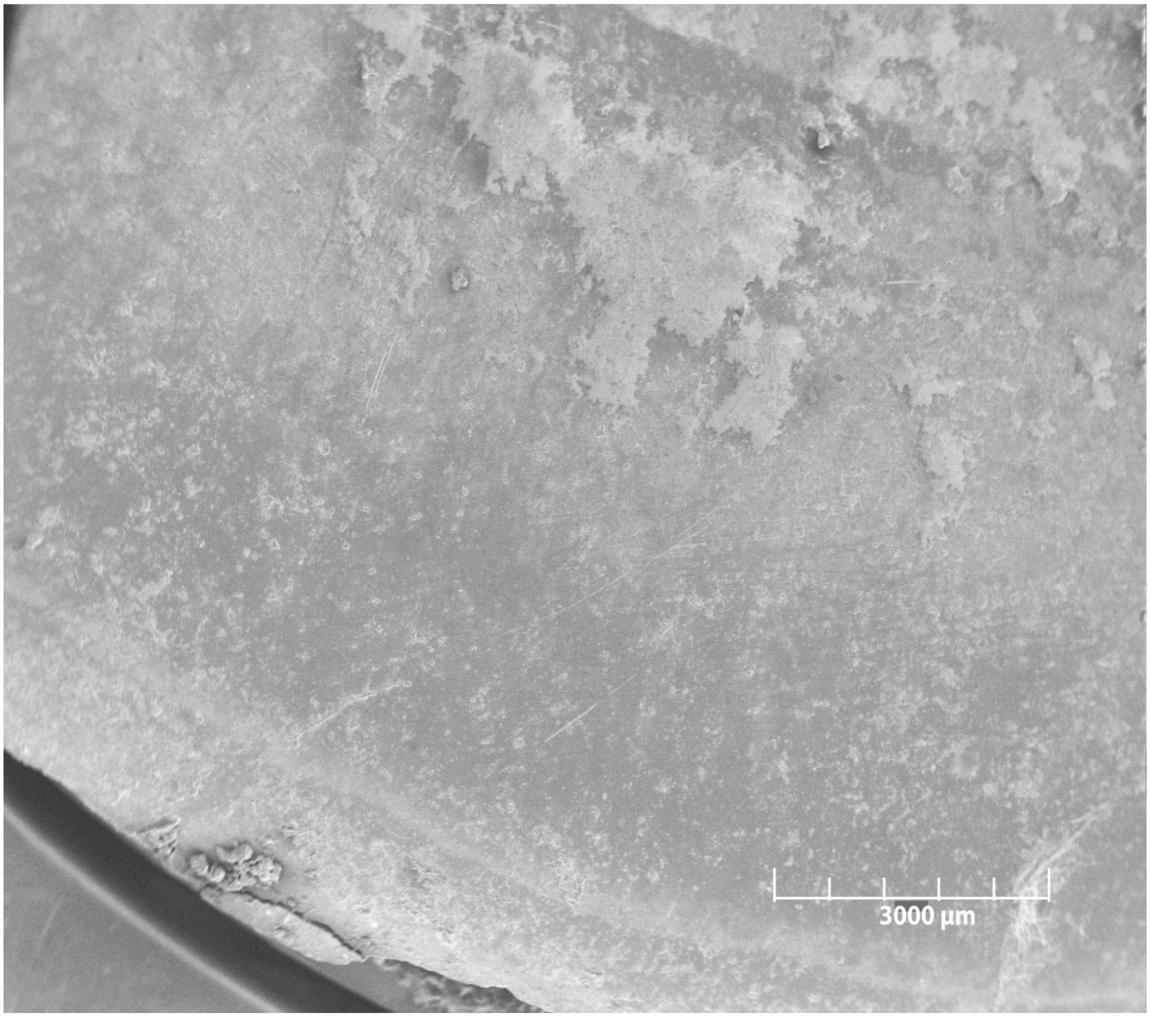

Figure A81, Rangia 1, 4 weeks

Figure A82, Rangia 1, 8 weeks

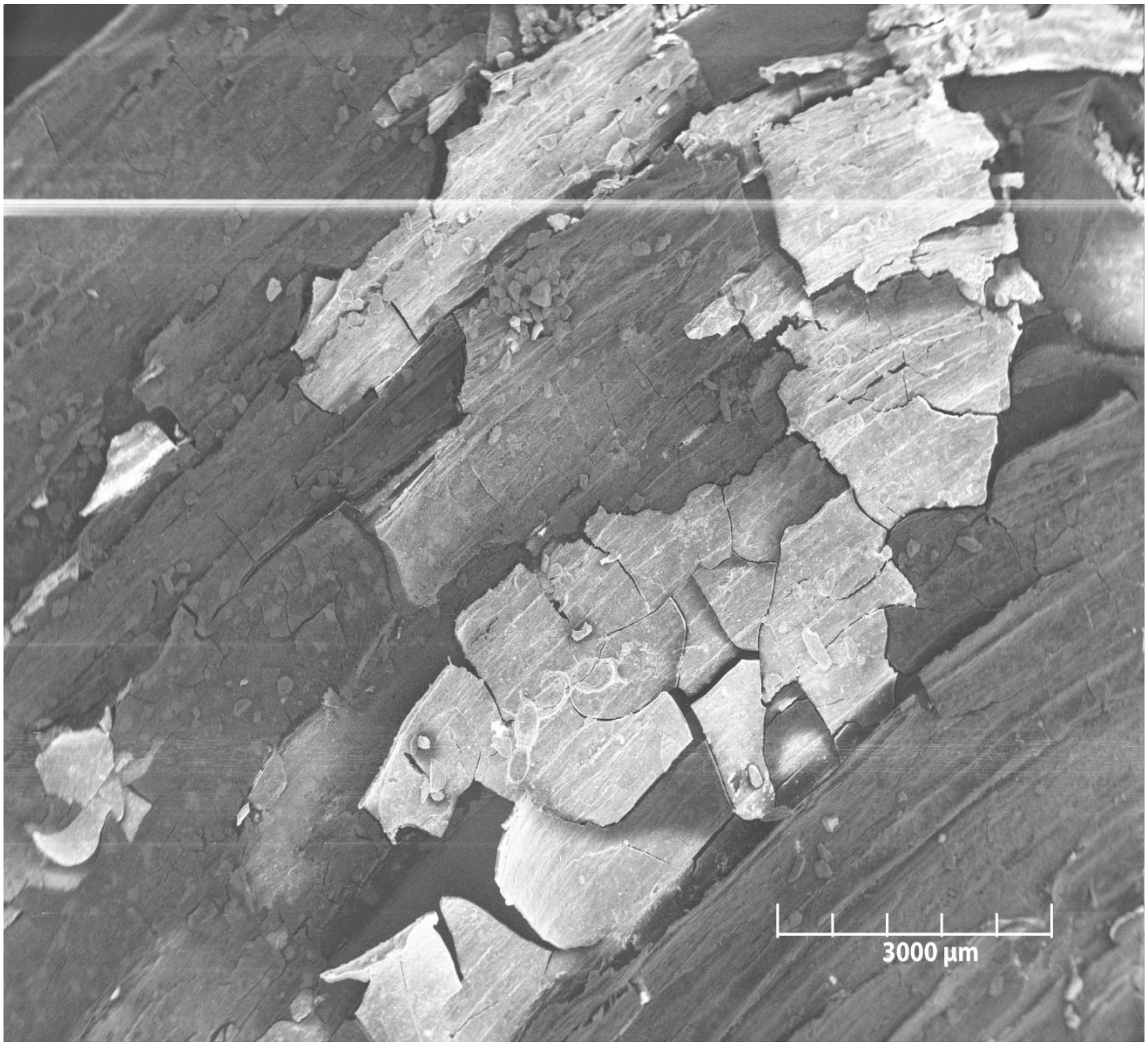

Figure A83, Rangia 2, 8 months

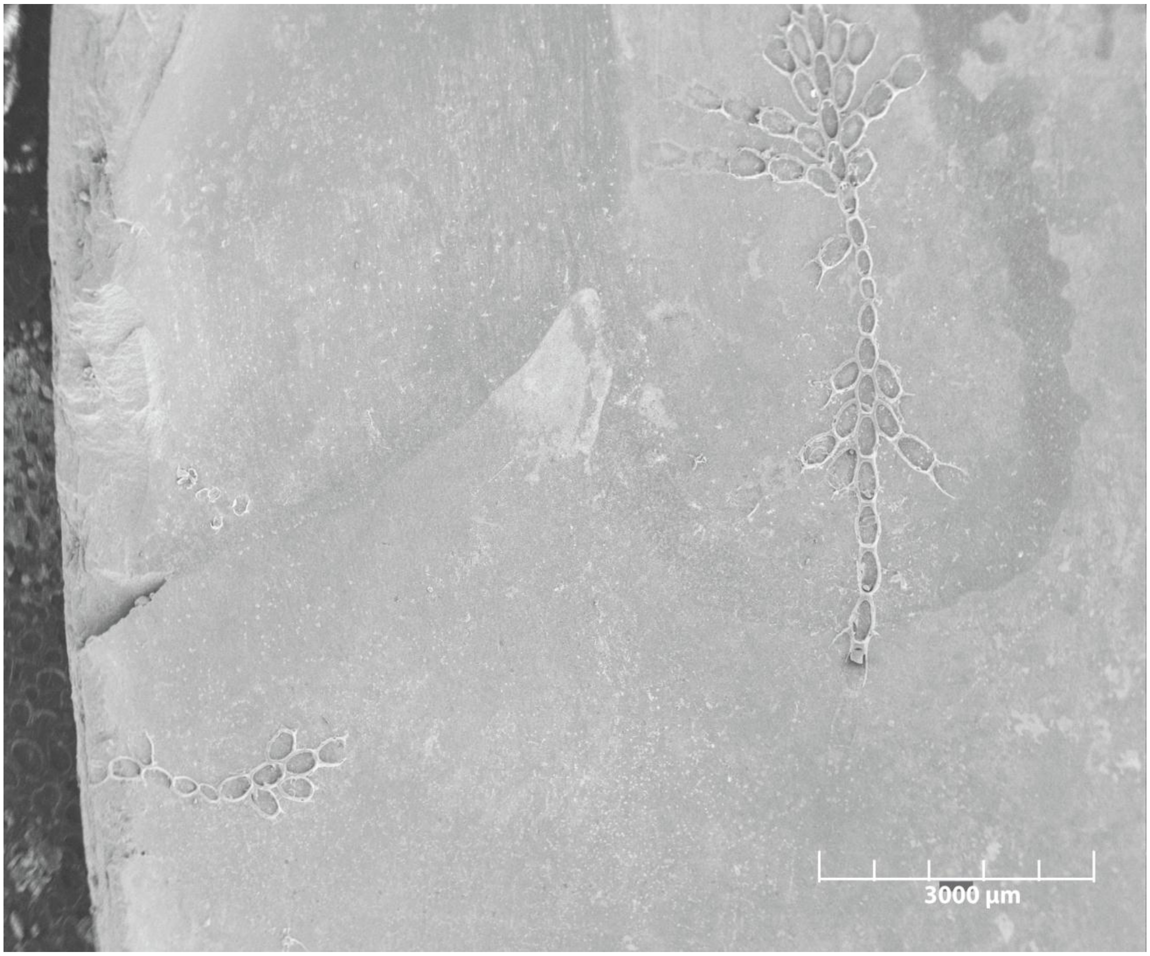

Figure A84, Rangia 3, 1 year

Figure A85, Rangia 3, 2 weeks

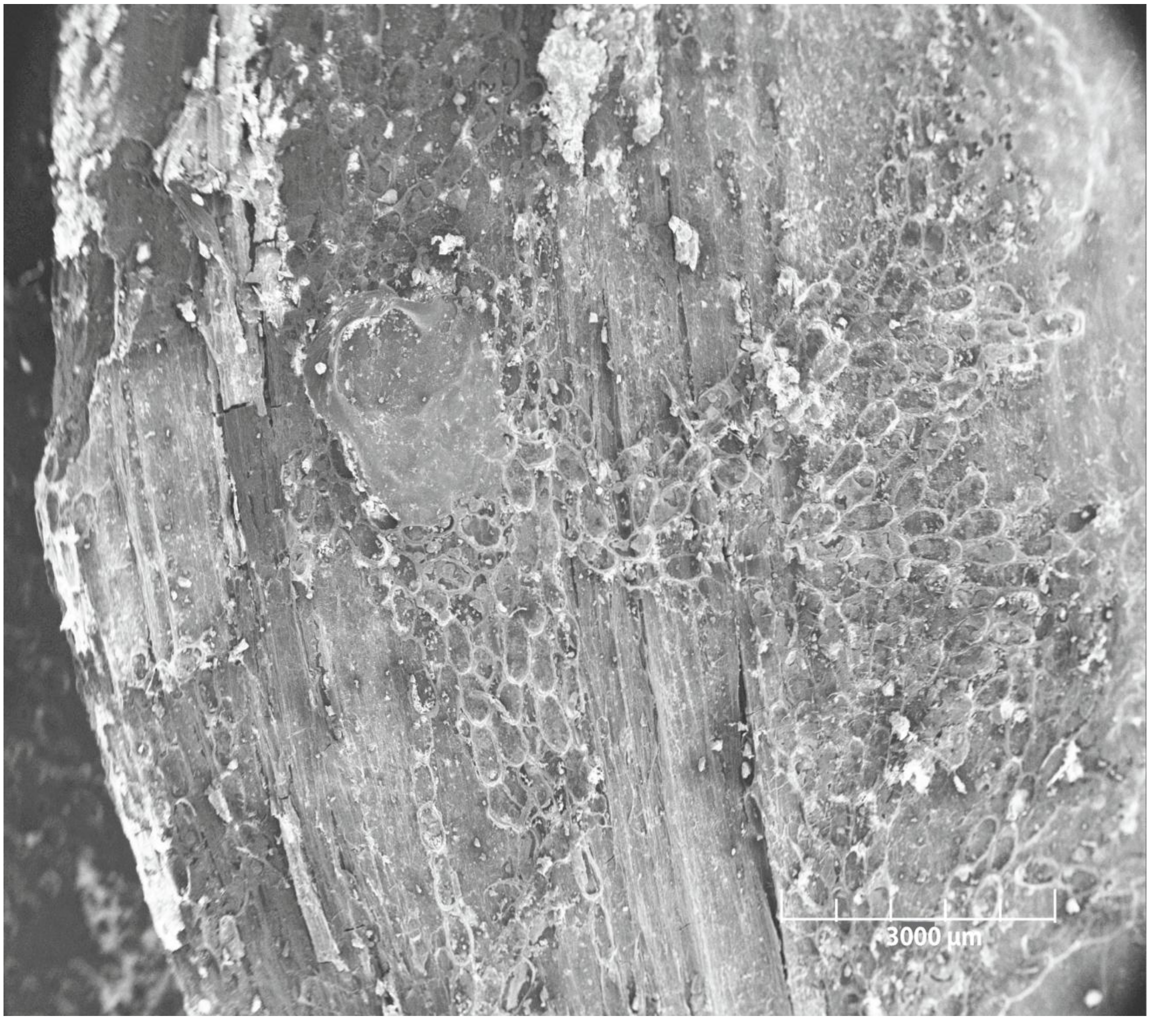

Figure A86, Rangia 3, 4 months

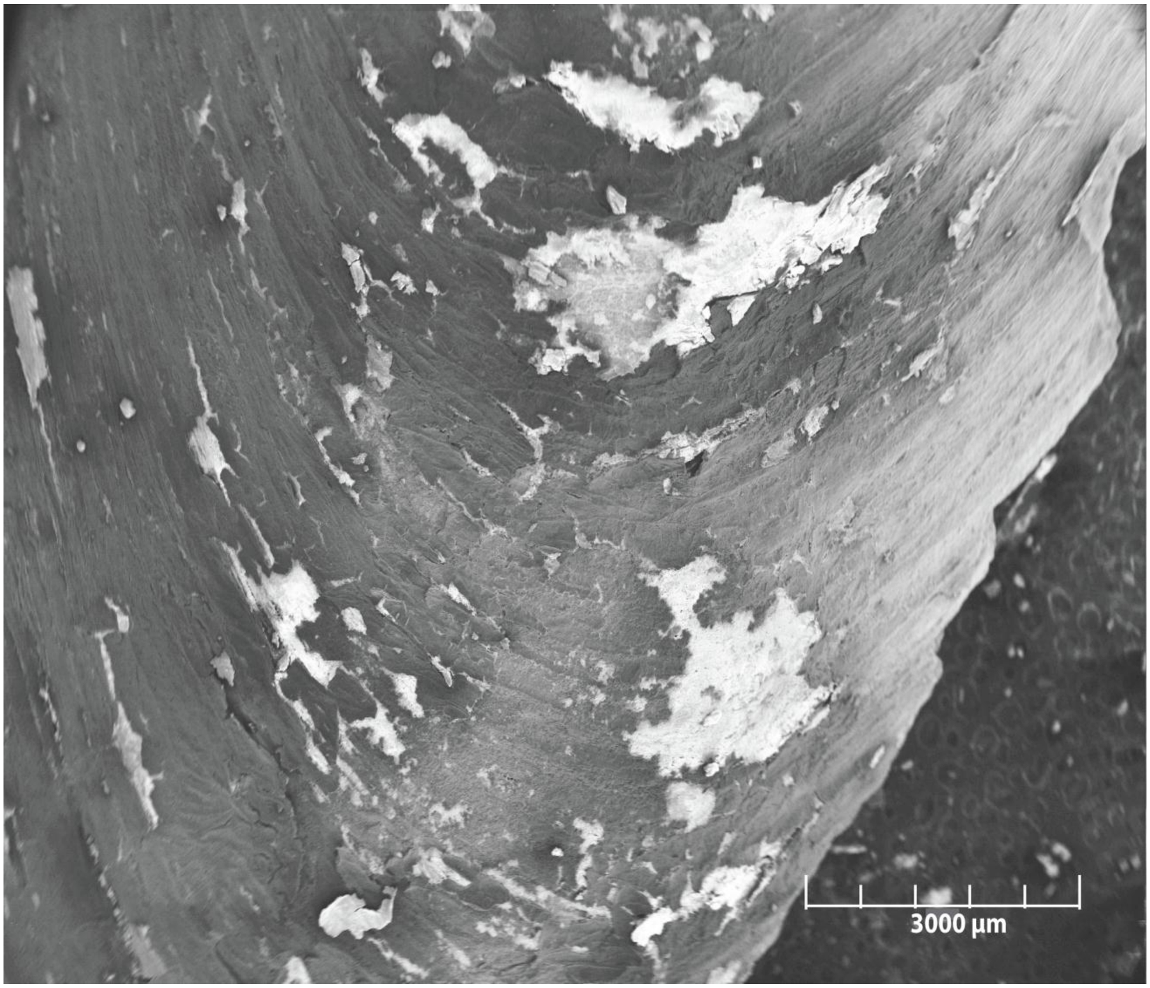

Figure A87, Rangia 3, 4 weeks

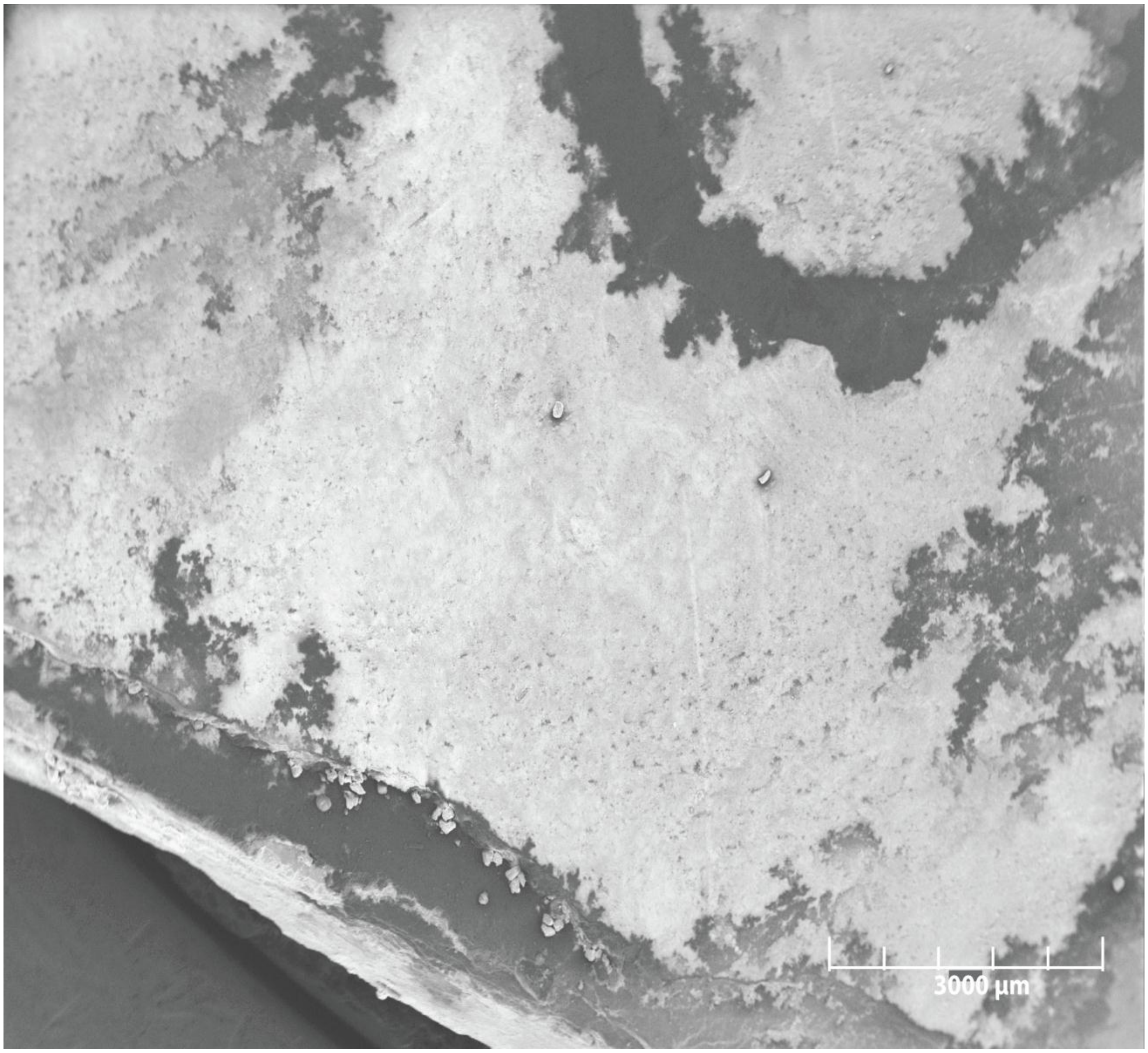

Figure A88, Rangia 4, 2 weeks

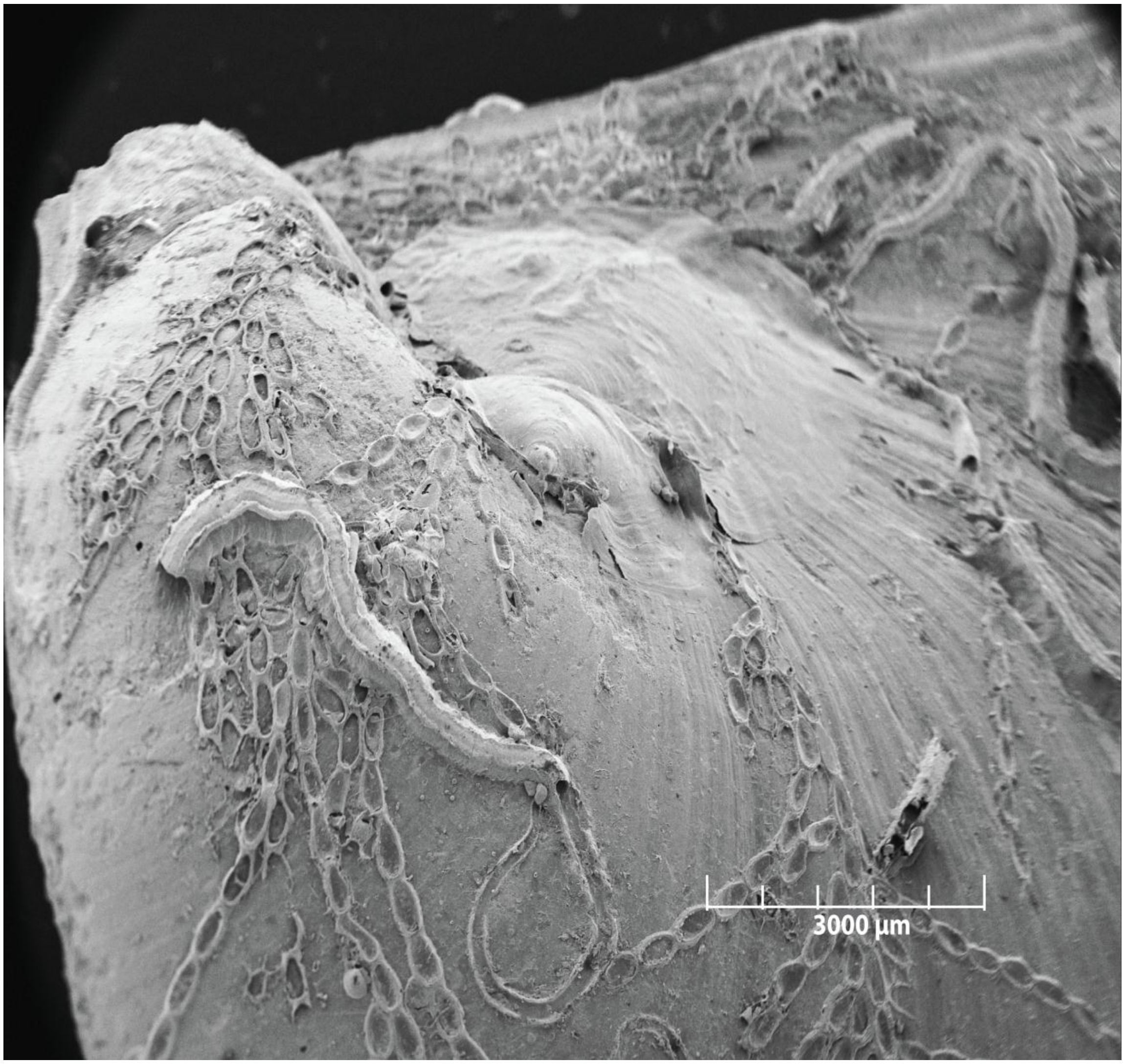

Figure A89, Rangia 4, 8 months

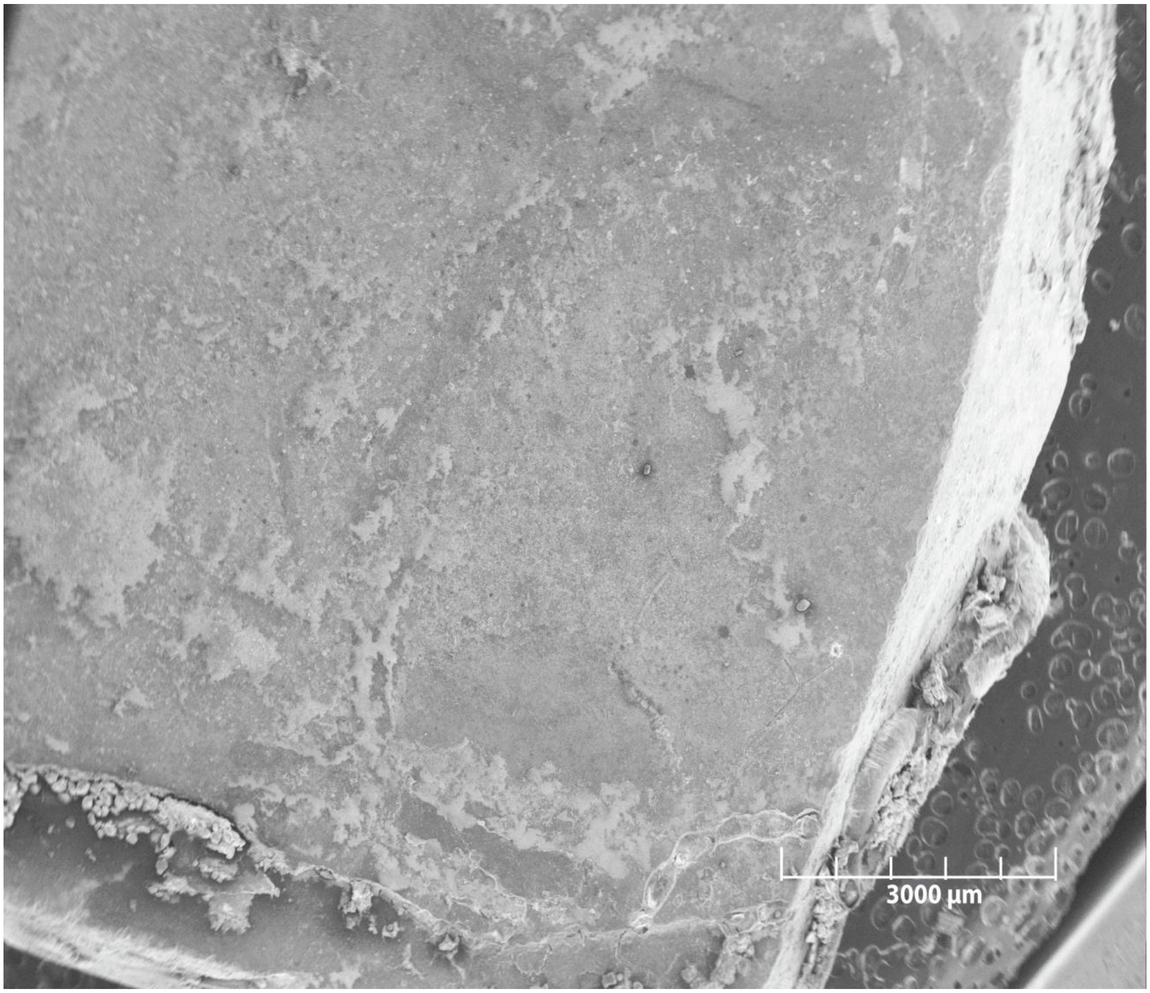

Figure A90, Rangia 4, 8 weeks

APPENDIX B

2 weeks	species	pre-mass (g)	post-mass (g)
	Ischadium 26	0.281406	0.278
	Crassostrea 8	1.0403	1.051
	Rangia 1	2.0688	2.07
	Rangia 3	3.7972	3.747
	Crassostrea 3	1.4052	1.406
	Ischadium 5	1.93839	1.97
	Ischadium 28	0.35943	0.358
	Rangia 4	1.94	1.935
	Ischadium 30	0.364739	0.367
	Ischadium 13	0.81021	0.822
	Amygdulum 9	0.054646	0.058068
	Macoma 24	0.012706	0.011815
	Macoma 1	0.011234	0.011187
	Amygdulum 14	0.028836	0.023752
	Mulinia 25	0.013091	0.012977
	Mulinia 13	0.004541	0.004517
	Macoma 13	0.018483	0.016336
	Mulinia 18	0.008584	0.008402
	Macoma 23	0.034287	0.032968

Table B1, Before and after masses of shells deployed for 2 weeks.

4 weeks	species	pre-mass (g)	post-mass (g)
	Rangia 3	5.4503	3.844
	Crassostrea 7	1.54	1.598
	Ischadium 24	0.435391	0.411
	Crassostrea 3	1.0448	1.04
	Ischadium 10	1.416055	1.409
	Rangia 1	4.728	5.49
	Ischadium 8	0.71973	0.855
	Ischadium 21	0.518894	0.5
	Amygdulum 18	0.030697	0.027955
	Macoma 8	0.011418	0.010657
	Mulinia 17	0.005679	0.005308
	Mulinia 4	0.00276	0.00266
	Amygdulum 12	0.026709	0.026157
	Mulinia 24	0.011257	0.011036
	Macoma 25	0.031741	0.030385
	Amygdulum 11	0.057886	0.05474

Table B2, Before and after masses of shells deployed for 4 weeks.

8 weeks	species	pre-mass (g)	post-mass (g)
	Rangia 1	5.3821	4.719
	Ischadium 27	0.260084	0.258
	Ischadium 16	0.755068	0.751
	Crassostrea 5	2.3819	2.546
	Crassostrea 8	2.3241	2.435
	Rangia 4	3.4227	3.538
	Ischadium 6	1.168135	1.158
	Macoma 26	0.011522	0.010616
	Mulinia 22	0.012497	0.012138
	Amygdulum 2	0.029761	0.02565
	Macoma 13	0.019091	0.01701
	Amygdulum 15	0.02141	0.016466
	Mulinia 12	0.003578	0.003336
	Macoma 29	0.02096	0.019824
	Mulinia 14	0.009504	0.008884
	Amygdulum 8	0.03528	0.03975
	Macoma 11	0.028236	0.023664

Table B3, Before and after masses of shells deployed for 8 weeks.

4 months	species	pre-mass (g)	post-mass (g)
	Rangia 3	3.7555	5.6
	Crassostrea 10	2.5362	2.435
	Rangia 1	5.4789	6.723
	Crassostrea 2	3.7594	3.814
	Ischadium 23	0.634534	0.617
	Ischadium 20	0.809488	0.802
	Ischadium 17	0.738332	0.72
	Ischadium 15	0.90003	0.881
	Crassostrea 7	2.7112	3.202
	Mulinia 16	0.006038	0.005894
	Mulinia 19	0.008102	0.008831
	Amygdulum 10	0.028895	0.00181
	Macoma 20	0.004032	0.018088
	Mulinia 20	0.006154	0.006098
	Amygdulum 3	0.023137	0.017617
	Macoma 30	0.021802	0.022017
	Macoma 15	0.023094	0.020764
	Amygdulum 17	0.028583	0.011814
	Macoma 16	0.028986	0.027791

Table B4, Before and after masses of shells deployed for 4 months.

8 months	species	pre-mass (g)	post-mass (g)
	Rangia 4	3.7107	3.45
	Rangia 2	2.7651	2.783
	Crassostrea 9	1.2084	1.246
	Crassostrea 5	1.1819	1.211
	Crassostrea 1	2.4107	3.142
	Ischadium 18	0.829506	0.0867
	Ischadium 19	0.69432	0.688
	Ischadium 11	0.72277	0.7
	Macoma 18	0.007612	0.003688
	Mulinia 7	0.003566	0.003794
	Mulinia 10	0.00341	0.013635
	Amygdulum 4	0.036982	0.022133
	Mulinia 28	0.055178	0.049515
	Macoma 12	0.022028	0.021519
	Macoma 2	0.011919	0.011535
	Amygdulum 13	0.029141	0.018475

Table B5, Before and after masses of shells deployed for 8 months.

1 year	species	pre-mass (g)	post-mass (g)
	Ischadium 9	1.178485	1.227
	Ischadium 3	1.70061	1.728
	Rangia 2	6.7458	6.24
	Crassostrea 2	3.0358	3.2
	Ischadium 29	0.312232	0.322
	Crassostrea 6	1.2177	1.956
	Ischadium 12	0.58011	0.568
	Rangia 3	2.6643	2.708
	Macoma 6	0.031354	0.013726
	Mulinia 1	0.001615	0.001348
	Mulinia 21	0.006565	0.006403
	Amygdulum 20	0.048888	0.041075
	Mulinia 26	0.014497	0.014501
	Amygdulum 5	0.051058	0.051379
	Macoma 19	0.015251	0.009459
	Macoma 5	0.013109	0.002853
	Mulinia 2	0.001732	0.000353

Table B6, Before and after masses of shells deployed for 1 year.